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Pleistocene non-passeriform landbirds from Shiriya, northeast Japan

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Located on the eastern margin of Eurasia, the Japanese Archipelago hosts a unique modern fauna of terrestrial vertebrates including landbirds which show a high proportion of endemic species/subspecies. Despite its potential importance in taxonomy and biogeography, the Pleistocene landbird fossil record has been scarce on Japanese islands, providing little information on the history of the unique fauna in the region. In this study, fossil remains of non-passeriform landbirds from the Middle–Late Pleistocene (Marine Isotope Stages [MIS] 9 and 5e) of Shiriya, northernmost Honshu Island, Japan, are revised with extensive osteological comparisons. As a result, the presence of at least six non-passeriform landbird species, represented by 71 specimens, was confirmed: *Syrnaticus* sp., *Coturnicini* gen. et sp. indet., *Columbidae* gen. et sp. indet., *Apus* sp., *Haliaeetus* sp., and *Accipitridae* gen. et sp. indet. The Shiriya paleoavifauna is the first substantial Pleistocene landbird fauna reported from the central Japanese islands so far, and suggests that the overall landbird fauna in northern Honshu in the last interglacial period (MIS 5e) was not drastically different from the present one, in contrast to the presence of several extinct land mammals and seabirds in the local fauna. The occurrence of *Syrnaticus* despite the supposedly colder climate in that time than today suggests that the distribution of modern *S. soemmerringii* might not be totally defined by climatic factors, but probably affected by a biogeographic barrier at the strait between Honshu and Hokkaido islands.

Key words: Aves, Phasianidae, Columbidae, Apodidae, Accipitridae, biogeography, Pleistocene, Japan.

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Introduction

The Japanese Archipelago, a chain of island arcs located on the eastern margin of Eurasia, hosts a remarkable vertebrate fauna due to its unique geographic location and geological history. Zoogeographically, it lies near the transition between the Palearctic and Oriental realms, which is sometimes referred to as the Sino-Japanese Realm to appreciate its distinctness (Holt et al. 2013a, b; but see also Kreft and Jetz 2013; Rueda et al. 2013). Concerning the modern landbird fauna, 47.2% of the currently recognized species/subspecies breeding in the Japanese Archipelago today is endemic to the region (Yamasaki 2017). In addition, Japanese islands might have been the origins of radiation in numbers of landbird lineages that now have broader geographic distributions (“reverse colonization”; Nishiumi and Kim 2015). As such, the Pleistocene landbird fossil record

in the Japanese Archipelago is of potential interest from the taxonomic and biogeographic perspectives.

The Japanese vertebrate fauna has evolved under the complex geomorphologic history of the Japanese Archipelago. The central part of the archipelago consists of four relatively large islands (Hokkaido, Honshu, Shikoku, and Kyushu islands) and numerous smaller ones surrounding them (hereafter collectively referred to as central Japanese islands). Although the central Japanese islands had been formed by back-arc rifting in the early–middle Miocene (Jolivet et al. 1994; Otofujii 1996), they are considered to have been partially connected to the Eurasian Continent on their southwestern part by land bridges in some part of the middle Miocene–earliest Pleistocene (until ~1.7 Ma), after which the separation from the continent became more pronounced (Chinzei 1991; Kitamura et al. 2001; Kitamura 2008). In some glacial periods in the Pleistocene, however,

the central Japanese islands were connected to the Eurasian Continent with two major pathways formed by land bridges, one through the Korean Peninsula and the other through Sakhalin Island, causing biotic interchanges with the continent (Kawamura 1998; Konishi and Yoshikawa 1999; McKay 2012; Nakazawa and Bae in press). In the Last Glacial Maximum, when the sea level was lower by ~120 m than in the present (e.g., Bintanja et al. 2005; Oba and Irino 2012), Honshu, Shikoku, and Kyushu islands were connected to each other (Paleo-Honshu–Shikoku–Kyushu Island) but probably separated from the continent, whereas Hokkaido Island was connected to the continent through Sakhalin Island (Paleo-Sakhalin–Hokkaido–Kuril Peninsula; Ota and Machida 1987; Ota and Yonekura 1987; Park et al. 2000; Chinzei and Machida 2001). Even in that time, the strait between Honshu and Hokkaido islands (Tsugaru Strait) remained, acting as a biogeographic barrier for terrestrial animals (Blakiston's Line; Blakiston and Pryer 1880; Milne 1881; Blakiston 1883; Tokuda 1941; Dobson 1994), perhaps except for those with high dispersal ability (e.g., large mammals; Kawamura 2007; Sawaura et al. 2018).

In general, Pleistocene fossils provide material evidences of temporal and geographic distributions of modern species, and play crucial roles in investigating many aspects of evolutionary histories of modern taxa and faunas. Relevant topics include speciation events (Selander 1965; Stewart 2002), species longevity, extinction and turnover (Brodkorb 1960; Tyrberg 2002, 2008b; Olson 2010; Meijer et al. 2015), and paleoclimate inference (Tyrberg 1999; Finlayson et al. 2008; Holm and Svenning 2014). Meta-analysis of compiled avian fossil records might be an attractive approach to these topics (e.g., Tyrberg 1999; Holm and Svenning 2014), but one should be cautious in interpreting the Pleistocene avian fossil record because there is a number of obstacles that may cause serious flaws in such analysis (Stewart 2002). One major issue prevalent in previously reported Quaternary paleoavifaunas is that fossils were identified without sufficient justifications. Many previous works report occurrences of species only in the form of faunal list and do not give descriptions or designations of fossil or comparative material, making it impossible to critically evaluate occurrence records in the literature. As many factors, including ontogenetic variation, sexual dimorphism, and geographic or temporal variation, may potentially influence quantitative and qualitative features of the avian skeleton (Stewart 2007), one should be cautious in choosing comparative specimens. Disregarding geographic variation may lead to incorrect taxonomic assignment (Storer 1992; Olson 2005). Identifications based on the distributions of modern species may lead to misidentification (Stewart 2005), or, for the purpose of biogeography, circular reasoning (Bever 2005; Nesbitt and Stocker 2008). Temporal variation (Northcote 1981; Ericson 1987; Stewart 2002) can potentially confound identification. In order to enable critical evaluation of identifications by future studies, it is advisable to clearly state the nature of the comparative material used, including species examined, quantity, and sexual and geographic coverage.

Despite its potential importance, the landbird fossil record in the Japanese Archipelago has been scarce. Apart from those in the Ryukyu Islands (e.g., Ono and Hasegawa 1985; Matsuoka 2000; Matsuoka and Hasegawa 2018) and archaeological sites (e.g., Nokariya and Ono 1980), most known localities yield only a few species (Takai 1962; Hasegawa 1964; Tomida 1978; Ono 1980; Rich et al. 1986), providing little concrete evidence for the history of landbird fauna in the region. In this respect, the Shiriya local fauna (Hasegawa et al. 1988), a Middle–Late Pleistocene vertebrate fauna recovered from fissure-filling deposits in Shiriya, northeast Japan, is of much interest. It consists of diverse land and marine vertebrates, including marine fish, amphibians, large carnivorous and herbivorous mammals, small land mammals, chiropterans, marine mammals, and various land- and seabirds. Hasegawa et al. (1988) listed 15 non-passeriform avian species for the Shiriya local fauna, including three landbirds (*Phasianus* sp., *Buteo buteo*, and *Haliaeetus* cf. *pelagicus*), but most of the avian material was left undescribed. Also, Hasegawa et al. (1988) did not give justification for identifications or designations of specimens for all species, necessitating a comprehensive revision.

In this report, as an outcome of a revision of the avian material from the Shiriya local fauna (Watanabe and Matsuoka 2015; Watanabe et al. 2016; JW, HM, and YH unpublished material), the non-passeriform landbird fossils from the Pleistocene of Shiriya are described, which turned out to belong to the following four families: Phasianidae, Columbidae, Apodidae, and Accipitridae. Detailed osteological descriptions are presented, in order to facilitate critical evaluation of identifications and comparison by future studies.

Institutional abbreviations.—ICM, Iida City Museum, Iida, Japan; KUGM, Department of Geology and Mineralogy, Kyoto University, Japan; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; NSMT AS, Avian Skeleton Collection, Department of Zoology, National Museum of Nature and Science, Tsukuba, Japan; NSMT PV, Vertebrate Paleontology Collection, Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan; USNM, Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; UWBM, Ornithology Collection, Burke Museum of Natural History and Culture, University of Washington, Seattle, USA; YIO, Yamashina Institute for Ornithology, Abiko, Japan.

Other abbreviations.—MIS, Marine Isotope Stage; lig., ligamentum/ligamenti; m., musculus/musculi; n., nervus/nervi.

Geological setting

The fossils described in this study came from fissure-filling deposits in Shiriya, Aomori Prefecture, northeastern Japan.

Geological background of the localities has been reviewed by Hasegawa et al. (1988) and Watanabe and Matsuoka (2015), thus only a brief summary would suffice here.

Shiriyā is located at the northeastern extremity of Honshu Island, Japan (41°24'N, 141°24'E; Fig. 1). The oldest rocks exposed in this area include slate, sandstone, chert, limestone, and limestone breccia (Murata 1962; Tsushima and Takizawa 1977; Matsuoka 1987; Sano et al. 2009), which comprise a pre-Tertiary tectonic complex (Kamada 2000). It is unconformably overlain by Miocene and Pliocene marine sedimentary rocks which yield no vertebrate remains (Tsushima and Takizawa 1977). On these basement rocks, a series of Middle–Late Pleistocene marine terraces is developed, each of whose age is correlated to a Marine Isotope Stage (MIS) based on dated volcanic ash layers interbedded in its deposits and relative altitudes to others (Koike and Machida 2001).

The fossils described here came from unconsolidated deposits that fill fissures or caves in limestone and limestone breccia bodies. Hasegawa et al. (1988) recognized four major vertebrate localities in the area: Loc. 1 (“Locality A” in Nakajima and Kuwano 1957); Loc. 2 (Shiriyā Second Quarry); Loc. 3 (Shiriyā Tunnel); and Loc. 4 (unnamed tunnel near Shikkari [also spelled Shitsukari]). The avian remains were recovered from Locs. 1–3.

No direct dating is available for the fossil localities, but the occurrence of marine vertebrates and the inclusion of marine-originated sediments indicate that the fossil-bearing layers had been deposited near the past sea level (Nakajima and Kuwano 1957; Nakajima 1958; Hasegawa et al. 1988). Therefore, the localities can be correlated to certain marine terrace surfaces; Loc. 2 (70–80 m above sea level) can be correlated to the Toei surface (65–80 m; MIS 9), and both Loc. 1 (~45 m above sea level) and Loc. 3 (~35 m) to the Tonamigaoka surface (35–45 m; MIS 5e; ages according to Koike and Machida 2001). These assignments are consistent with the occurrence of land mammals typical of the Pleistocene of the central Japanese islands (Hasegawa 1972; Kamei et al. 1988).

Material and methods

The avian fossils from Shiriyā temporarily stored in ICM, KUGM, and NSMT PV were examined, including those figured by Hasegawa et al. (1988). Bone scraps were also screened for identifiable specimens. The fossils from Loc. 1 were collected by Zenji Nakajima in 1950's, whereas those from locs. 2 and 3 were collected by YH and others in 1960 and 1987. All specimens described in this study are now formally deposited in NSMT PV. All specimens had been recovered as isolated bones after water-sieving of sediments. All limb bones described are skeletally mature, as confirmed from inspection of surface textures and other features that are indicative of ontogenetic stages (Tumarkin-Deratzian et al. 2006; Watanabe and Matsuoka 2013; Watanabe 2018a, b).

Comparison was primarily made with modern avian

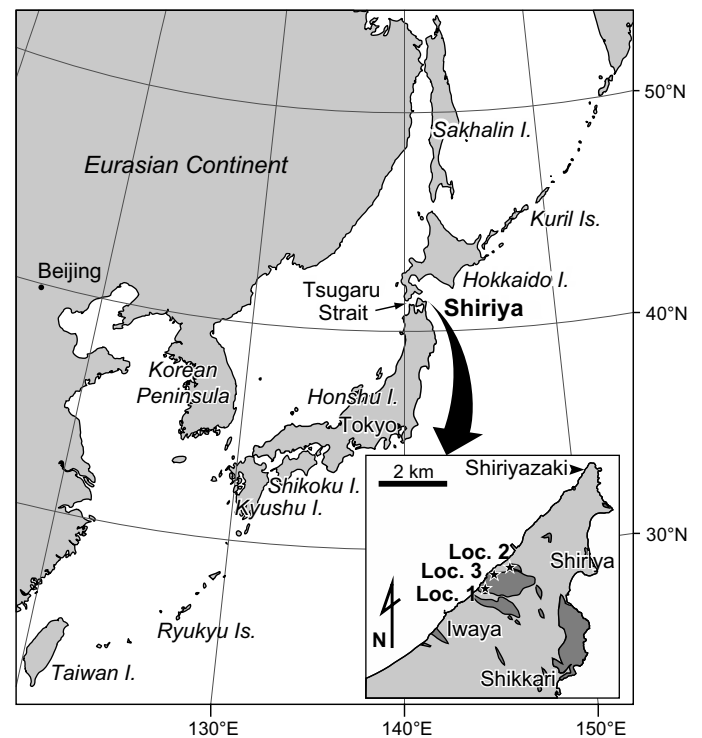


Fig. 1. Geographic location of Shiriyā localities. Landmarks mentioned in the text are also indicated. Inset (41°24'N, 141°24'E) shows major fossil localities mentioned in the text (stars; after Hasegawa et al. 1988). Dark grey indicates distribution of limestone/limestone breccia bodies (after Tsushima and Takizawa 1977). Abbreviations: I., island; Is., islands.

skeletons stored in KUGM, MVZ, NSMT AS, UWBM, USNM, and YIO. A list of comparative material is given in Appendix 1. The status and distribution of modern birds in the Japanese Archipelago were largely taken from *Check-list of Japanese Birds* (The Ornithological Society of Japan 2012). Osteological terminology generally follows Baumel and Witmer (1993), but that of Howard (1929) is also used when appropriate. The term “omal” is used to designate the upper/cranial end of the coracoid. Measurements were taken with digital calipers (Mitutoyo, Kawasaki, Japan) and values rounded to the nearest 0.1 mm are reported. Size and proportion of fossils were compared with those of comparative specimens through visual inspection of scatter plots of dimensions.

Systematic palaeontology

Class Aves Linnaeus, 1758

Order Galliformes Temminck, 1820

Family Phasianidae Horsfield, 1821

Remarks.—For the comparative purpose, the classification of modern taxa within this family follows del Hoyo and Collar (2014). Hasegawa et al. (1988) included *Phasianus* sp. in their faunal list, but did not designate any specimens.

Subfamily Phasianinae Horsfield, 1821

Tribe Phasianini Horsfield, 1821

Genus *Syrmaticus* Wagler, 1832

Syrmaticus sp.

Fig. 2A, B, E, F, G–K.

Material.—Loc. 3, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 24531, 24532, left omal and sternal coracoids, respectively; NSMT PV 24533–24535, two right and one left proximal humeri, respectively; NSMT PV 24536, right distal humerus; NSMT PV 24537 left humeral shaft; NSMT PV 24538, right ulnare; NSMT PV 24539, worn proximal phalanx of the right major wing digit. Locality unrecorded, Shiriya, Aomori Prefecture, Japan; Middle–Late Pleistocene (~MIS 9/5e): NSMT PV 24540, tip of premaxilla; NSMT PV 24541, 24542, proximal and distal fragments of right carpometacarpus, respectively.

Measurements.—See Table 1 and Fig. 3.

Description.—One well preserved proximal end of the humerus was recovered (Fig. 2A). The fossil is characterized by a narrow dorsal tricipital fossa (the fossa dorsal to the crus dorsale fossae), which is pointed proximally with a faint dorsal margin and only slightly excavates the distal margin of the caput humeri in its ventral part. The combination of these states is apparently unique to Phasianini (the dorsal tricipital fossa is wider and excavates the caput humeri more deeply in Rollulinae and most other tribes within Phasianinae except Pavonini). The fossil differs from Pavonini in a proximodistally thinner tuberculum ventrale that lacks a distinct attachment scar just ventral to its tip (which is characteristically present at this position in Pavonini). Within Phasianini, the fossil agrees only with *Syrmaticus* (except *S. reevesii*) in weak development of the incisura capitis (in *Chrysolophus*, *Phasianus*, *Crossoptilon*, *Catreus*, *Lophura*, and *S. reevesii*, the incisure is wider and

deeper, and excavates the proximal margin of the tuberculum ventrale; Fig. 2C₁, D₁). Two other fragmentary proximal humeri are tentatively referred to the same species, based on the consistency of size and observable features.

Another phasianid humerus preserving the distal half of the bone (Fig. 2B) is referred to the same species as the proximal end with which it is roughly consistent in size. In the fossil, the processus flexorius is well developed distally, as in Coturnicini, Lophophorini, Phasianini, and Tetraonini (except *Meleagris*). The fossil differs from Coturnicini in the absence of a concavity on the epicondylus ventralis just caudal to the pit for the m. pronator superficialis (see below), and from most members of Tetraonini (except *Perdix* and *Meleagris*) in less craniocaudal compression of the body.

An omal end of the coracoid preserving the processus acrocoracoideus (Fig. 2J) and a sternal end of the coracoid with a worn angulus lateralis (Fig. 2K) are tentatively referred to this species, with which they are consistent in size. In the fossil, the impressio lig. acrocoracohumeralis is dorsoventrally thick and developed as a deep groove with distinct margins. This state is characteristic to some members of Phasianini and Tetraonini (except *Perdix*, *Meleagris*, and *Bonasa*) among phasianids. The omal end differs from Tetraonini and agrees with Phasianini in a relatively straight profile of the tuberculum brachiale in medial view (in Tetraonini, its dorsal tip is produced sternally to give a concave profile to the tuberculum brachiale). The fossil differs from *Phasianus* and agrees with *Syrmaticus* in a relatively poorly developed ventral part of the processus acrocoracoideus (in *Phasianus*, it is strongly elevated from the shaft and produced medially, with the ventral margin of the tuberculum brachiale protruding as medially as the dorsal margin; Fig. 2C₃, D₃, J₃). The sternal protrusion of the processus lateralis observed in the fossil sternal end, the most sternal point of which is lying even sternally than the

Table 1. Measurements (in mm) of *Syrmaticus* sp. from the upper Pleistocene of Shiriya compared with Recent *Syrmaticus soemmerringii* and *Syrmaticus reevesii*. Abbreviations: BFAH, breadth of the facies articularis humeralis; D, craniocaudal depth; DCH, craniocaudal depth of the caput humeri; GDB, greatest distal breadth; n, number of individuals; W, dorsoventral width; WSA, mediolateral width of the sternal articulation.

Elements	<i>Syrmaticus</i> sp.	<i>Syrmaticus soemmerringii</i>			<i>Syrmaticus reevesii</i>		
		n	range	mean	n	range	mean
Coracoid							
BFAH	10.6, –	18	9.7–13.3	11.7	9	10.9–13.1	11.9
WSA	–, 10.4	19	9.6–13.9	11.6	9	10.8–13.7	11.9
Humerus							
proximal W	19.2, –, –	20	16.6–19.9	17.8	10	18.6–21.8	20.3
DCH	7.8, 7.5, 7.9	20	6.4–8.2	7.3	10	7.0–8.9	8.0
W midshaft	7.1, 6.5	19	6.3–7.9	7.0	10	6.7–8.7	7.9
D midshaft	5.8, 5.3	19	4.7–6.4	5.4	10	5.5–6.9	6.2
distal W	13.9, –	19	12.2–14.5	13.0	10	13.6–16.2	14.8
distal D	8.4, –	19	7.4–8.9	8.0	10	8.4–11.0	9.4
GDB	14.6, –	19	12.8–15.3	13.8	10	14.4–17.5	15.8
Carpometacarpus							
distal W	4.1	12	3.5–4.5	3.9	10	3.7–4.5	4.1
distal D	6.7	12	6.1–7.2	6.6	10	6.8–8.0	7.4

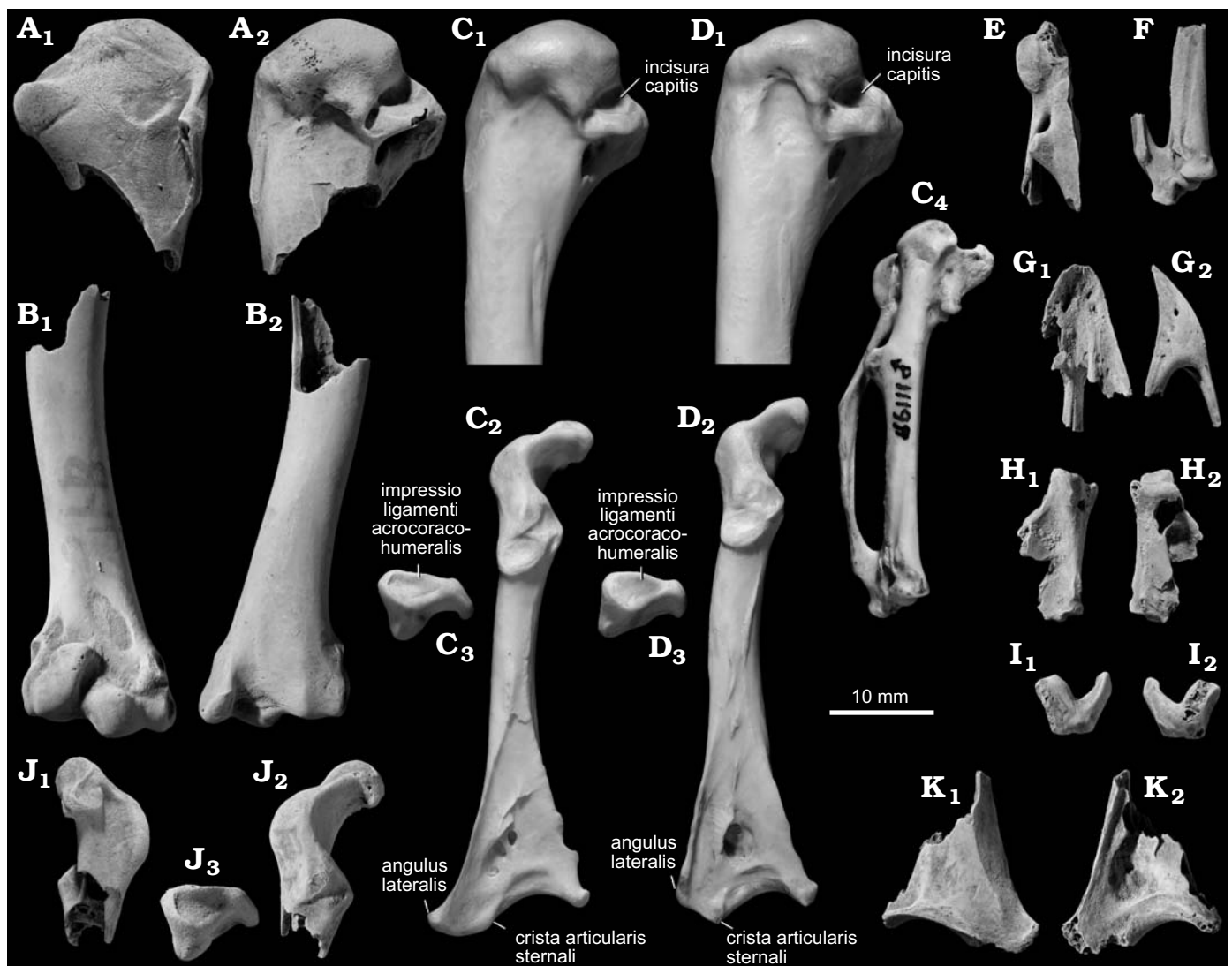


Fig. 2. Plesianid bird *Syrmaticus* sp. from the upper Pleistocene of Shiriya, Japan (A, B, E, F, H–L), compared with Recent *Syrmaticus soemmerringii* (Temminck, 1830) (C) and Recent *Phasianus colchicus* Linnaeus, 1758 (D). A. NSMT PV 24535, left humerus in cranial (A₁) and caudal (A₂) views. B. NSMT PV 24536, right humerus in cranial (B₁) and caudal (B₂) views. C. MVZ 49764, left humerus in caudal view (C₁), left coracoid in dorsal (C₂) and omal (C₃) views, right carpometacarpus in dorsal view (C₄). D. MVZ 68327, left humerus in caudal view (D₁), left coracoid in dorsal (D₂) and omal (D₃) views. E, F. NSMT PV 24541 and NSMT PV 24542, respectively, right carpometacarpi in dorsal view. G. NSMT PV 24540, premaxilla in ventral (G₁) and left lateral (G₂) views. H. NSMT PV 24539, proximal phalanx of right major wing digit in dorsal (H₁) and ventral (H₂) views. I. Right ulnare (NSMT PV 24538), in distal (I₁) and proximal (I₂) views. J. Left coracoid (NSMT PV 24531), in ventral (J₁), dorsal (J₂), and omal (J₃) views. K. Left coracoid (NSMT PV 24532), in ventral (K₁) and dorsal (K₂) views. Fossils coated with ammonium chloride.

lateral end of the crista articularis sternalis (Fig. 2K), is apparently unique to Phasianini (in most other phasianids, the latter is the most sternal point in the coracoid). This feature is most pronounced in *Syrmaticus* within Phasianini, with which the fossil agrees (Fig. 2C₂, D₂).

One carpometacarpus preserving the proximal symphysis and processus intermetacarpalis (Fig. 2E), another preserving the distal symphysis and articular surfaces (Fig. 2F), a proximal phalanx of major wing digit lacking the caudodistal part (Fig. 2H), one moderately worn ulnare (Fig. 2I), and a tip of premaxilla (Fig. 2G) are tentatively referred to this species. The fossils are too fragmentary for definitive identification,

although they are consistent with modern species of the genus in size and proportions.

Remarks.—This genus includes several modern species of pheasants which are distributed in China, northern Indochina, Taiwan, and most central Japanese islands (except for Hokkaido Island). As far as observed in this study, few qualitative features observable in the Shiriya material were found useful in distinguishing species within the genus, except for the development of the incisura capitis of the humerus noted above; the incisure is deep and wide in *S. reevesii* and the other genera of the tribe Phasianini, whereas it is narrower and shallower in the other modern species of *Syrmaticus*. Although it is tempting to specu-

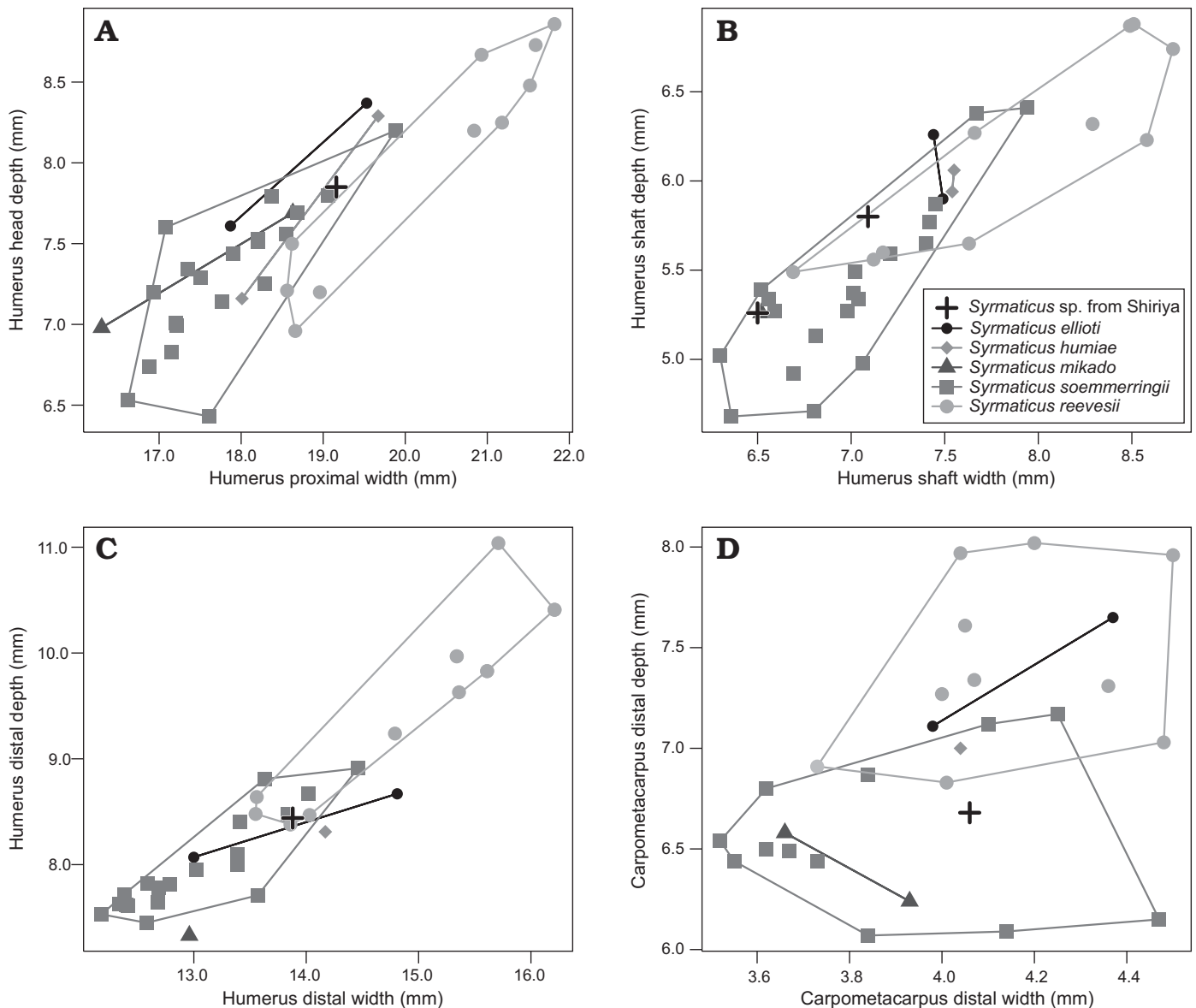


Fig. 3. Bivariate scatter plots of Recent and fossil species of *Syrmaticus*: proximal (A) and distal (C) humeral, humeral shaft (B), and carpometacarpal (D) measurements.

late that this character reflects the phylogenetic relationship (e.g., the state observed in *S. reevesii* represents a primitive condition within *Syrmaticus*), the available evidence is inconclusive; most recent molecular phylogenetic analyses (Zhan and Zhang 2005; Wang et al. 2013; Jiang et al. 2014; Hosner et al. 2016) recovered either *S. soemmerringii* or *S. reevesii* as the most basal divergences within the genus, but the branching orders for these species have not been well resolved. In any way, the Shiriya fossils clearly agree with the group including *S. soemmerringii*, *S. mikado*, *S. ellioti*, and *S. humiae*. Although most dimensions of the Shiriya material are consistent with those of modern *S. soemmerringii*, the only species that occur on the central Japanese islands today, the sample size is too small to allow definitive assignment to any of the modern species (Fig. 3), let alone identification to the subspecific level.

Two extinct species of *Syrmaticus* have been named so far: *S. phasianoides* (Jánossy, 1991) from the upper Miocene of Hungary (Jánossy 1991; Zelenkov 2016) and *S. kozlovae* Kurochkin, 1985, from the upper Miocene–lower Pliocene of Mongolia (Kurochkin 1985; Zelenkov and Kurochkin 2010). According to published dimensions (Zelenkov 2016), *S. phasianoides* is larger than any modern species of the genus, thus would be larger than the Shiriya material as well. According to published dimensions and descriptions (Zelenkov and Kurochkin 2010), *S. kozlovae* is slightly smaller than the Shiriya material, and further differs from it in certain osteological features of the distal humerus, including a less distally protruding processus flexorius (see Zelenkov and Kurochkin 2010).

The fossil record of the modern species of the genus is scanty. *Syrmaticus soemmerringii* has been identified

from several Pleistocene localities in the central Japanese islands (Takai 1962; Nokariya and Ono 1980; Ono 1980), but little justifications were given in these previous reports. As *S. soemmerringii* had once been included in *Phasianus* in some past editions of the *Check-list of Japanese Birds* (e.g., The Ornithological Society of Japan 1974), this species may possibly be represented by identifications labeled as “*Phasianus* sp.” by Japanese authors (e.g., Ono in Rich et al. 1986). Although *S. reevesii* had been reported from the Pleistocene of Choukoutien (also known as Zhoukoudian), China (Shaw 1935), a later, more comprehensive report of the paleoavifauna (Hou 1993) did not mention this species.

Modern *S. soemmerringii* is the only species of the genus that naturally occurs in the central Japanese islands, where it is an endemic, resident breeder. Lying at the north-eastern tip of Honshu Island, Shiriya is at the northern limit of the natural distribution of the species; it does not occur in Hokkaido Island except as an introduced breeder (The Ornithological Society of Japan 2012). If the Shiriya material represents that species, the occurrence would indicate that the species had spread throughout Honshu Island by the Late Pleistocene (MIS 5e), assuming that the genus originated in the continental Asia as indicated by the distribution and phylogeny of modern and fossil species (Zhan and Zhang 2005; Zelenkov and Kurochkin 2010).

Hasegawa et al. (1988) included *Phasianus* sp. in their faunal list for the Shiriya local fauna without designating any specimens. The examination of the entire avian material from Shiriya in this study could not identify specimens certainly referable to *Phasianus* rather than *Syrnaticus*. Although some fragmentary specimens within the material might possibly represent a species of the former genus, the absence of diagnostic specimens seems a sufficient reason to retract the occurrence of *Phasianus* sp. from the Shiriya local fauna.

Tribe Coturnicini Reichenbach, 1848

Coturnicini gen. et sp. indet.

Fig. 4.

Material.—Loc. 3, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 24543, right distal humerus. Locality unrecorded, Shiriya, Aomori Prefecture, Japan; Middle–Late Pleistocene (~MIS 9/5e): NSMT PV 24544–24546, one right and two left distal tibiotarsi, respectively; NSMT PV 24547, right proximal tarsometatarsus.

Measurements.—See Table 2.

Description.—One distal end of the humerus was recovered (Fig. 4A). The fossil can be referred to Coturnicini (*Coturnix*, *Synoicus*, *Tetraogallus*, *Alectoris*, *Ammoperdix*, *Perdica*, and *Pternistis*) by the following features that are apparently unique within Phasianidae: the concavity of the ventral surface of the epicondylus ventralis caudal to the pit for the m. pronator superficialis (Fig. 4A₂), and the fossa m. brachialis being narrow and restricted to the ventral half of the shaft (the latter feature is exceptionally absent

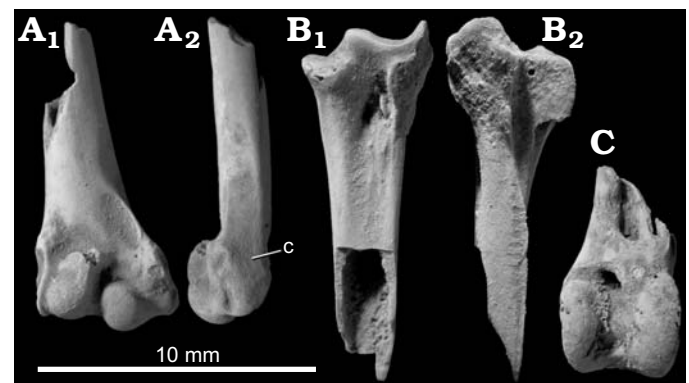


Fig. 4. Coturnicini gen. et sp. indet. from the upper Pleistocene of Shiriya, Japan. A. NSMT PV 24543, right humerus in cranial (A₁) and ventral (A₂) views. B. NSMT PV 24547, tarsometatarsus in dorsal (B₁) and medial (B₂) views. C. NSMT PV 24545, left tibiotarsus in cranial view. Fossils coated with ammonium chloride. Abbreviation: c, concavity on the ventral surface of epicondylus ventralis (see text).

in *Tetraogallus*). Within Coturnicini, the fossil agrees with *Coturnix* and *Synoicus* and differs from the other genera examined in the presence of a marked depression on the cranioproximal margin of the condylus dorsalis. Furthermore, the fossil differs from *Tetraogallus* in the ventral position of the fossa m. brachialis mentioned above, and from *Perdica* in a less abrupt dorsoventral expansion of the shaft toward the distal end. In these features, the fossil is consistent with *Coturnix* and *Synoicus*, which are osteologically rather similar to each other.

Three fragmentary distal ends of the tibiotarsus (Fig. 4C) and one proximal end of the tarsometatarsus (Fig. 4B) of a small phasianid were recovered. As few taxonomically useful characters can be observed in these fossils, they are tentatively assigned to the same species with the humerus.

Remarks.—The overall consistency of size suggests that only one species of Coturnicini is represented in the Shiriya

Table 2. Measurements (in mm) of Coturnicini gen. et sp. indet. and Columbidae gen. et sp. indet. from the upper Pleistocene of Shiriya. Abbreviations: D, craniocaudal (for humerus) or dorsoventral (for leg elements) depth; GDB, greatest distal breadth; W, dorsoventral (for humerus) or mediolateral (for leg elements) width.

Elements	Coturnicini gen. et sp. indet.	Columbidae gen. et sp. indet.
Humerus		
W midshaft		4.9, –
D midshaft		3.6, –
GDB	5.2	
distal W	5.1	
distal D	3.0	
Tibiotarsus		
distal W	4.3, 4.3, 4.2	
distal D	4.4, 4.4, 4.1	
Tarsometatarsus		
proximal W	4.8	
proximal D	4.5	

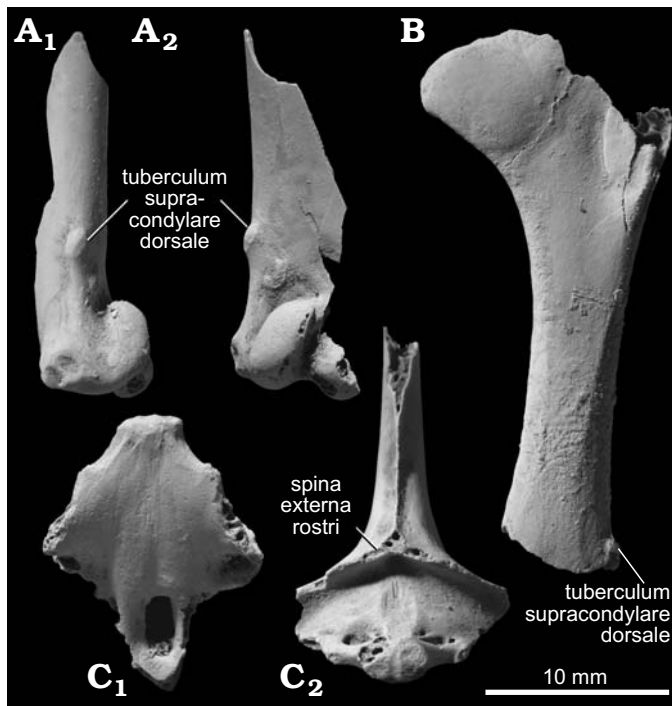


Fig. 5. Columbidae gen. et sp. indet. from the upper Pleistocene of Shiriya, Japan. **A.** NSMT PV 24551, right humerus in dorsal (**A₁**) and cranial (**A₂**) views. **B.** NSMT PV 24552, left humerus in cranial view. **C.** NSMT PV 24553 sternum in ventral (**C₁**) and cranial (**C₂**) views. Fossils coated with ammonium chloride.

material. Although the known elements could not be separated from modern *Coturnix japonica*, the only species of quail that occurs on the central Japanese islands today, it is not certain if it can be differentiated from other species of *Coturnix* or *Synoicus*, which are distributed throughout the Old World and Oceania.

Order Columbiformes Garrod, 1874

Family Columbidae Leach, 1820

Columbidae gen. et sp. indet.

Fig. 5.

Material.—Loc. 3, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 24551, sternal fragment; NSMT PV 24552, left humeral shaft; NSMT PV 24553, right distal humerus.

Measurements.—See Table 2; sternum: no formal measurement possible.

Description.—One moderately worn sternal fragment preserving the rostral area and the dorsal half of the pila carinae was recovered (Fig. 5C). The spina externa rostri is broken away, but at least was originally present, unlike in some genera of Raphinae, including *Otidiphaps* and *Ptiliophaps*. The spina interna rostri is moderately developed cranially, and is wider laterally than it is thick dorsoventrally.

One humeral shaft preserving proximally from the distal extents of the crista bicapitalis and tuberculum dorsalis

and distally to the tuberculum supracondylare dorsale, and another distal fragment of the humerus preserving the area around the tuberculum supracondylare dorsale and condylus dorsalis were recovered (Fig. 5A, B).

Remarks.—Due to the rather fragmentary nature of the specimens, it was not possible to assign any of them to the subfamilial or generic level. The consistency of size suggests that only one species is represented, which would be similar in size to moderate-sized pigeons and turtle-doves, e.g., modern *Streptopelia orientalis*.

Order Apodiformes Peters, 1940

Family Apodidae Olphe-Galliard, 1887 (1836)

Remarks.—The family Hemiprocnidae is sometimes treated as a subfamily of Apodidae (Hemiprocninae), but can be readily distinguished from Apodidae in numbers of osteological features, including weak medial protrusion of the processus acrocoracoideus of the coracoid (which is strongly protruded medially in Apodidae) and a caudally bowed os metacarpale minor of the carpometacarpus (straighter in Apodidae).

Subfamily Apodinae Olphe-Galliard, 1887 (1836)

Genus *Apus* Scopoli, 1777

Apus sp.

Fig. 6A, C, D.

Material.—Loc. 3, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 24548, left coracoid; NSMT PV 24549, left carpometacarpus; NSMT PV 24550, proximal phalanx of right major wing digit.

Measurements.—See Table 3 and Fig. 7.

Description.—One left coracoid with a worn angulus lateralis was recovered (Fig. 6A). The fossil differs from the members of Cypseloidinae (*Streptoprocne* and *Cypseloides*) in the narrowness of a notch on the dorsal part of the sternal margin of the tuberculum brachiale (the notch being dorsoventrally broad and often deep in Cypseloidinae). It differs from Collocaliini (*Collocalia* and *Aerodramus*) and agrees with Apodini (*Aeronautes*, *Tachornis*, *Cypsiurus*, *Tachymarptis*, and *Apus*) and to a lesser extent with Chaeturini (*Hirundapus* and *Chaetura*) in an elongated and slit-like medioventral opening of the foramen n. supracoracoidei (which is omo-sternally narrower in Collocaliini). It also differs from Chaeturini in the absence of a strong constriction of the neck (in Chaeturini, the neck is constricted and the processus acrocoracoideus is slanted medially). Within Apodini, the fossil agrees with *Tachornis*, *Tachymarptis*, and *Apus* and differs from *Aeronautes*, *Panyptila*, and *Cypsiurus* in a relatively omal position of the dorsal opening of the foramen n. supracoracoidei (which is distinctly offset sternally from the omal margin of the processus supracoracoidei in the latter genera). The fossil has a characteristic profile of the sternal articulation surface, where the medioventral margin is

strongly produced, the dorsal flange is lying rather medially (Fig. 6B₂), and the dorsolateral margin is strongly concave. This condition is apparently unique to *Tachymarptis* and *Apus* within Apodidae. The single coracoid of *Tachymarptis* examined (*T. melba*, USNM 559068) is distinct from the fossil in the presence of a prominent ridge on the ventral margin of the shaft leading from the lateral part of the sternal end to the ventral margin of the sulcus supracoracoideus. The fossil is indistinguishable from *A. apus* and *A. pacificus* in both dimensions and qualitative characters.

One complete left carpometacarpus was recovered (Fig. 6C). The fossil differs from Cypseloidinae in a cranially lying sulcus tendinosus in dorsal view (Fig. 6C₂, B₃); which is lying on the caudal half of the distal shaft in Cypseloidinae and the absence of a constriction of the distal shaft of the os metacarpale minor (the constriction is present around the distal one-fifth in Cypseloidinae). It differs from Collocaliini and Chaeturini and agrees with Apodini in a strong expansion of the os metacarpi minor near the distal symphysis. Collocaliini further differ in a deeper distal part of the fossa supratrochlearis, and *Hirundapus* differs in a cranially positioned processus pisiformis. Within Apodini, the fossil agrees with *Tachymarptis* and *Apus* in a relatively small processus alularis whose proximal margin is not slanted proximally. The fossil carpometacarpus is consistent in size with the coracoid described above, thus is referred to the same species with it.

A distal phalanx of the major wing digit lacking the distal articular surface was recovered (Fig. 6D). Although relatively few taxonomically useful characters were detected for this element, the fossil differs from *Streptoprocne* in the absence of a strong convexity on the cranial surface of the proximal shaft, from *Cypseloides* in the absence of a prominent swell on the middle part on the cranial surface, from *Aerodramus* in the absence of a strong constriction at the base of the distal extension of the caudal margin, from Chaeturini on one hand and *Aeronautes*, *Tachornis*, and *Panyptila* on the other in a moderately developed depression on the ventral surface (which is deeper and narrower in the former group and shallower in the latter), and from most genera of the family except *Hirundapus*, *Tachymarptis*, and *Apus* in the broadness of the tip of the distal extension of the caudal margin. Therefore, the fossil is consistent only with *Tachymarptis* and *Apus* among the genera compared. Its size is consistent with the carpometacarpus described above.

Remarks.—The genus *Apus* is distributed throughout the Old World (chiefly in Africa), and includes c. 15 modern species. Although recent authors tend to separate *Tachymarptis* from it (Päckert et al. 2012; Dickinson and Remsen 2013; del Hoyo and Collar 2014), there seems to be relatively few osteological differences between the two genera, as far as concerning the elements known for the Shiriya material (but see the feature of the coracoid mentioned above).

Only two species of the genus occur on Japanese islands today: *A. pacificus* and *A. nipalensis*. The Shiriya material is larger than the latter species and consistent in size with the

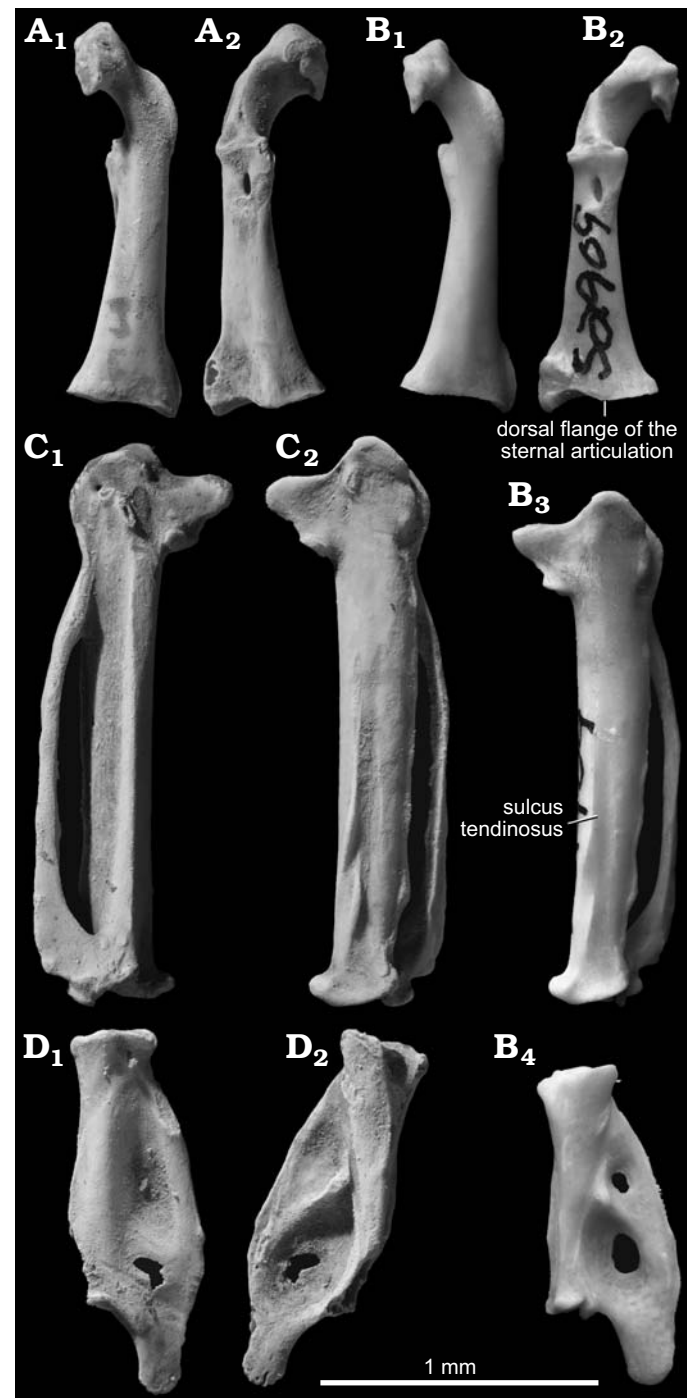


Fig. 6. Apodid bird *Apus* sp. from the upper Pleistocene of Shiriya, Japan (A, C, D), compared with Recent *Apus pacificus* (Latham, 1801) from Russia (B). A. NSMT PV 24548, left coracoids in ventral (A₁) and dorsal (A₂) views. B. UWM 46958, left coracoid, in ventral (B₁) and dorsal (B₂) views; left carpometacarpus in dorsal view (B₃); proximal phalanx of left major wing digit in dorsal view (B₄). C. NSMT PV 24549, left carpometacarpus in ventral (C₁) and dorsal (C₂) views. D. NSMT PV 24550, proximal phalanx of right major wing digit in ventral (D₁) and dorsal (D₂) views. Fossils coated with ammonium chloride.

former (Table 3; Fig. 7). However, the fossils cannot be distinguished from other modern species of the genus, including *A. apus* whose modern range spans over northern China.

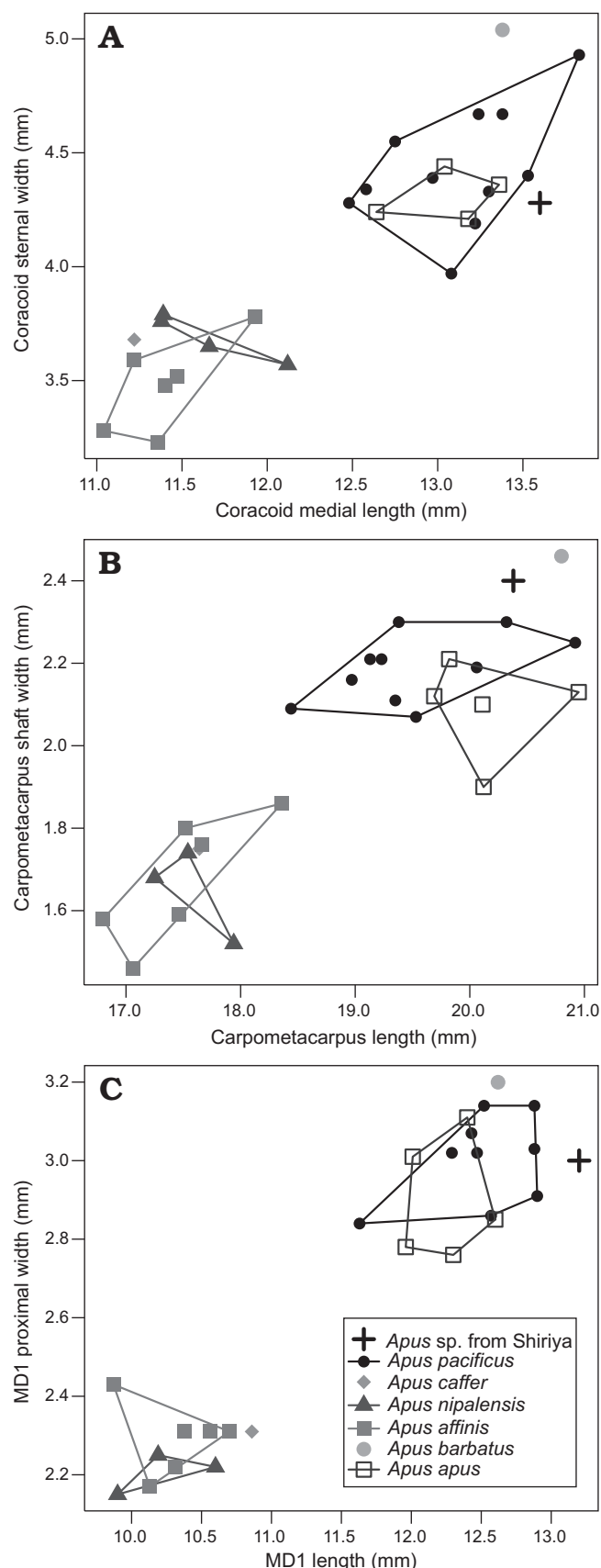


Fig. 7. Bivariate scatter plots of Recent and fossil species of *Apus* coracoidal (A), carpometacarpal (B), and proximal phalanx of major wing digit (C) measurements. MD1, proximal phalanx of major wing digit.

The fossil record of Apodidae was reviewed by Mlíkovský (1989, 2002) and Boev (2000). Several extinct species/subspecies of *Apus* have been described from Neogene deposits in Europe. *Apus wetmorei* Ballmann, 1976, and *A. gaillardii* (Ennouchi, 1930) are known from the upper Miocene of Italy and France, respectively. The former species was described as a species in size of modern *A. caffer*, and the latter was estimated to be smaller than modern *A. apus* (according to dimensions given by Harrison 1984). Therefore, these species would be smaller than the species represented by the Shiriya material, although no elements are known in common.

Apus apus palapus Jánossy, 1974, known from the Lower Pleistocene of Austria (Jánossy 1974) and possibly of Hungary (Jánossy 1978), is a temporal subspecies of *A. apus* which differs from the modern form in osteometric proportions. On its original description (Jánossy 1974), it was only compared with modern *A. apus* and *A. pallidus*. As such, despite Jánossy's (1974) conjecture, it is not certain if that subspecies can be osteologically differentiated from modern *A. pacificus*. *Apus baranensis* Jánossy, 1978, is known from the upper Miocene–Lower Pleistocene of Hungary and Bulgaria (Jánossy 1978; Boev 2000; Kessler 2010). Being smaller than *A. affinis*, it is unlikely to be represented by the Shiriya material (see also Fig. 7). Although *A. baranensis* was synonymized with *A. wetmorei* by Mlíkovský (2002) based on the putative similarity of size alone, this act has been doubted by Zelenkov (2017) who mentioned the actual difference in size. *Apus submelba* Jánossy, 1972, known from several Middle–Late Pleistocene localities in Europe (Jánossy 1972, 1978; Mourer-Chauviré 1975; Tyrberg 2008a), is considered closely related to modern *Tachymarptis* (formerly *Apus*) *melba*, and indeed has been considered synonymous with the modern species by Mlíkovský (2002). The species might be better moved to *Tachymarptis*, if it is a distinct species and that genus deserves separation from *Apus*. In any way, published dimensions (Jánossy 1972) indicate that it was larger than the Shiriya material. Apart from these extinct forms, remains of modern species of the genus are known from numerous Quaternary localities throughout the Old World (e.g., Tyrberg 1998, 2008a; Harvati et al. 2013; Val 2016).

Order Accipitriformes Vieillot, 1816

Family Accipitridae Vigors, 1824

Remarks.—Hasegawa et al. (1988) included *Haliaeetus* cf. *pelagicus* and *Buteo buteo* in their faunal list, for each of which one specimen was figured. They are re-identified here as follows.

Genus *Haliaeetus* Savigny, 1809

Haliaeetus sp.

Fig. 8A, D, E–R.

1988 *Haliaeetus* cf. *pelagicus* (Pallas, 1811); Hasegawa et al. 1988: pl. 7: 13.

Table 3. Measurements (in mm) of *Apus* sp. from the upper Pleistocene of Shiriya, compared with Recent *A. pacificus*, *A. apus*, and *A. nipalensis*. “Diagonal length” of the proximal phalanx of major wing digit refers to the greatest distance from the proximal articular surface to the distocaudal end (not to the distal articular surface, which is lacking in the fossil). Abbreviations: D, craniocaudal (for wings bones) or dorsoventral (for coracoid) depth; n, number of individuals; PP, processus procoracoideus; W, dorsoventral (for wing bones) or mediolateral (for coracoid) width; WSA, width of sternal articulation.

Elements	<i>Apus</i> sp.	<i>Apus pacificus</i>			<i>Apus apus</i>			<i>Apus nipalensis</i>		
		n	range	mean	n	range	mean	n	range	mean
Coracoid										
medial length	13.6	11	12.5–13.8	13.1	4	12.6–13.4	13.1	4	11.4–12.1	11.6
W below PP	1.9	12	1.4–1.9	1.7	5	1.6–1.8	1.7	4	1.2–1.4	1.3
D below PP	1.5	12	1.3–1.6	1.5	5	1.3–1.6	1.5	4	1.1–1.4	1.2
WSA	4.3	12	4.0–4.9	4.4	5	4.2–4.4	4.3	4	3.6–3.8	3.7
Carpometacarpus										
length	20.4	10	18.4–20.9	19.5	5	19.7–20.9	20.1	3	17.2–17.9	17.6
proximal W	2.2	10	2.1–2.3	2.2	5	2.1–2.3	2.2	3	1.7–1.8	1.8
proximal D	6.0	10	5.5–5.9	5.7	5	5.5–5.8	5.6	3	4.7–4.8	4.7
W midshaft	2.4	10	2.1–2.3	2.2	5	1.9–2.2	2.1	3	1.5–1.7	1.6
D midshaft	2.5	10	2.3–2.7	2.5	5	2.3–2.6	2.5	3	1.8–2.0	2.0
distal W	3.0	10	2.7–3.2	2.9	5	2.6–2.9	2.7	3	2.2–2.4	2.3
Proximal phalanx of major wing digit										
diagonal length	13.2	10	9.3–12.9	12.2	5	12.0–12.6	12.3	3	9.9–10.6	10.2
proximal W	3.0	9	2.8–3.1	3.0	5	2.8–3.1	2.9	3	2.1–2.2	2.2
proximal D	3.0	9	2.7–2.8	2.7	5	2.6–2.9	2.8	3	2.2–2.3	2.2

Material.—Loc. 1, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 24554, right humeral shaft and NSMT PV 24555, terminal phalanx of left first toe (?). Loc. 2, Shiriya, Aomori Prefecture, Japan; middle Pleistocene (~MIS 9): NSMT PV 24556, left coracoid without sternal end; NSMT PV 24557, sternal end of right coracoid; NSMT PV 24558, left distal humerus; NSMT PV 24559–24561, right ulnar shafts; NSMT PV 24562, left distal ulna; NSMT PV 24563, 24564, left distal carpometacarpus; NSMT PV 24565, left alular phalanx; NSMT PV 24566, 24567, fragmentary right tibiotarsal shafts; NSMT PV 24568, right distal tibiotarsus, NSMT PV 24569–24580, terminal pedal phalanges. Loc. 3, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 24581, incomplete cranium; NSMT PV 24582, right humeral shaft; NSMT PV 24583, right distal humerus; NSMT PV 24584, left proximal ulna; NSMT PV 24585, left distal radius; NSMT PV 24586, left ulna; NSMT PV 24587, left femoral shaft; NSMT PV 19010, right distal tibiotarsus; NSMT PV 24588, terminal phalanx of right first toe (?). Locality unrecorded, Shiriya, Aomori Prefecture, Japan; Middle–Late Pleistocene (~MIS 9/5e): NSMT PV 24589, left coracoid shaft; NSMT PV 24590, 24591, left and right distal tibiotarsi, respectively; NSMT PV 24592–24597, terminal pedal phalanges.

Measurements.—See Table 4 and Fig. 9.

Description.—One cranium preserving a part of the frontals, the dorsal margin of the foramen magnum, and both tympanic cavities was recovered (Fig. 8A). In the fossil, there is only a shallow depression rostral to the tympanic cavity, ventral to the fossa temporalis, where a prominent excavation, from which the quadratic articulations are distinctly el-

evated, is present in most accipitrids (Fig. 8A₃, B₃, C₃). This feature is apparently unique to *Haliaeetus* and *Haliastur*, as well as to some Gypaetinae (*Pernis*, *Aviceda*, *Polyboroides*, and *Gypaetus*). The crania in the latter group are much deeper dorsoventrally for its width (except *Gypaetus*) and characterized by a narrower fossa temporalis. In addition, the fossil differs from some other large-bodied accipitrid genera, including *Aquila* and *Aegypius*, in weaker lateroventral extension of the cranial roof over the laterocaudal margin of the cotyla quadratica squamosi.

Three coracoid shafts, the most complete one of which preserves the dorsal part of the processus acrocoracoideus and entire processus procoracoideus (Fig. 8D, E), are referred to the same species as the cranium. The fossils have a stocky profile compared to most accipitrids, while lacking extensive pneumatization along the entire cranial margin of the sulcus supracoracoideus (which is seen in Gypini), agreeing with *Harpia*, *Aquila*, *Haliastur*, *Milvus*, *Butastur*, *Haliaeetus*, and *Ichthyophaga*. Among those genera, the fossils differ from *Harpia* and *Aquila* and agree with the others in weak development of the sternal margin of the facies articularis claviculæ, which is developed as a prominent ridge on the medial surface of the processus acrocoracoideus in the former group (Fig. 8B₄, C₄). The fossils differ from the coracoid of *Butastur* in having a single pneumatic fovea caudal to the dorsal tip of the tuberculum brachiale (whereas *Butastur* has a pair of foveae in the same position).

One moderately worn proximal part of the ulna, with the olecranon broken away, was recovered (Fig. 8H). The shaft is relatively shallow craniocaudally, agreeing only with some species of *Haliaeetus*, including *H. albicilla*, *H.*

Table 4. Measurements (in mm) of *Haliaeetus* sp. from the middle–upper Pleistocene of Shiriya, compared with Recent *Haliaeetus pelagicus*, *Haliaeetus albicilla*, and *Haliaeetus leucocephalus*. Abbreviations: BFAH, breadth of the facies articularis humeralis; CNT, crista nuchalis transversa; D, depth perpendicular to width; IMB, impressio musculi brachialis; FT, fossa temporalis; n, number of individuals; PP, processus procoracoideus; PPO, processus postorbitalis; W, dorsoventral (for wing bones) or mediolateral (for the other elements) width.

Elements	<i>Haliaeetus</i> sp. from Shiriya	<i>Haliaeetus pelagicus</i>			<i>Haliaeetus albicilla</i>			<i>Haliaeetus leucocephalus</i>		
		n	range	mean	n	range	mean	n	range	mean
Skull										
W PPO	> 69	3	65.5–71.0	68.2	4	58.6–63.5	60.7	3	61.4–67.9	64.3
cranium W	48.6	3	46.7–48.6	47.6	3	41.5–45.3	42.8	3	43.7–46.5	44.8
W across CNT	58.7	3	56.6–57.5	57.1	4	50.6–57.3	53.4	3	54.8–60.4	57.4
Coracoid										
BFAH	21.1, –	9	21.3–25.1	23.0	9	18.3–23.2	20.8	3	18.9–22.2	20.6
W below PP	10.4, 12.3	9	10.3–12.2	11.2	9	9.2–11.0	10.0	3	9.4–10.7	9.9
D below PP	13.2, –	9	13.3–16.8	14.5	9	10.9–14.0	12.5	3	12.0–13.3	12.5
Humerus										
W midshaft	16.5, 15.5	4	16.6–17.9	17.2	6	13.2–16.3	14.7	3	14.9–16.4	15.5
D midshaft	14.6, 12.9	4	14.0–16.2	14.8	6	11.9–14.7	13.4	3	13.3–14.9	13.9
Ulna										
proximal W	24.2, –, –	3	25.2–27.0	25.8	5	20.8–24.3	22.5	3	22.1–25.3	23.3
W below IMB	13.8, 14.5, –	3	13.2–14.3	13.9	5	11.4–13.8	12.4	3	12.3–13.4	12.9
D below IMB	10.2, 10.8, –	3	11.0–11.8	11.5	5	9.2–12.1	10.7	3	10.4–12.2	11.1
distal D	–, –, 19.0	3	18.9–19.8	19.4	5	15.9–18.5	16.9	3	17.1–19.2	17.9
Radius										
distal W	16.4	3	16.5–17.9	17.0	4	13.9–16.4	15.0	3	14.8–16.9	15.6
distal D	8.0	3	7.9–9.2	8.5	4	6.7–8.0	7.2	3	6.9–8.1	7.6
Carpometacarpus										
distal W	> 11.7	3	12.7–13.1	12.9	5	11.2–12.6	11.9	3	11.8–13.2	12.3
Femur										
W midshaft	> 13.8	7	13.4–15.3	14.6	8	11.1–13.3	12.0	3	11.7–13.1	12.3
Tibiotarsus										
narrowest W	13.9, 16.1, 13.2, –, –	3	12.2–14.8	13.8	5	9.9–12.9	11.3	3	10.9–12.4	11.8
narrowest D	8.1, 8.7, 8.9, –, –	3	7.8–9.8	8.8	5	6.9–8.7	7.6	3	7.3–8.1	7.7
distal W	22.0, 22.5, –, 27.0, –, 21.0	3	22.9–26.7	25.0	5	17.8–21.7	19.7	3	19.6–22.3	20.7
distal D	14.9, 16.4, –, 18.4, –	2	18.0, 21.6	–	5	13.2–15.6	14.3	3	14.4–16.5	15.1

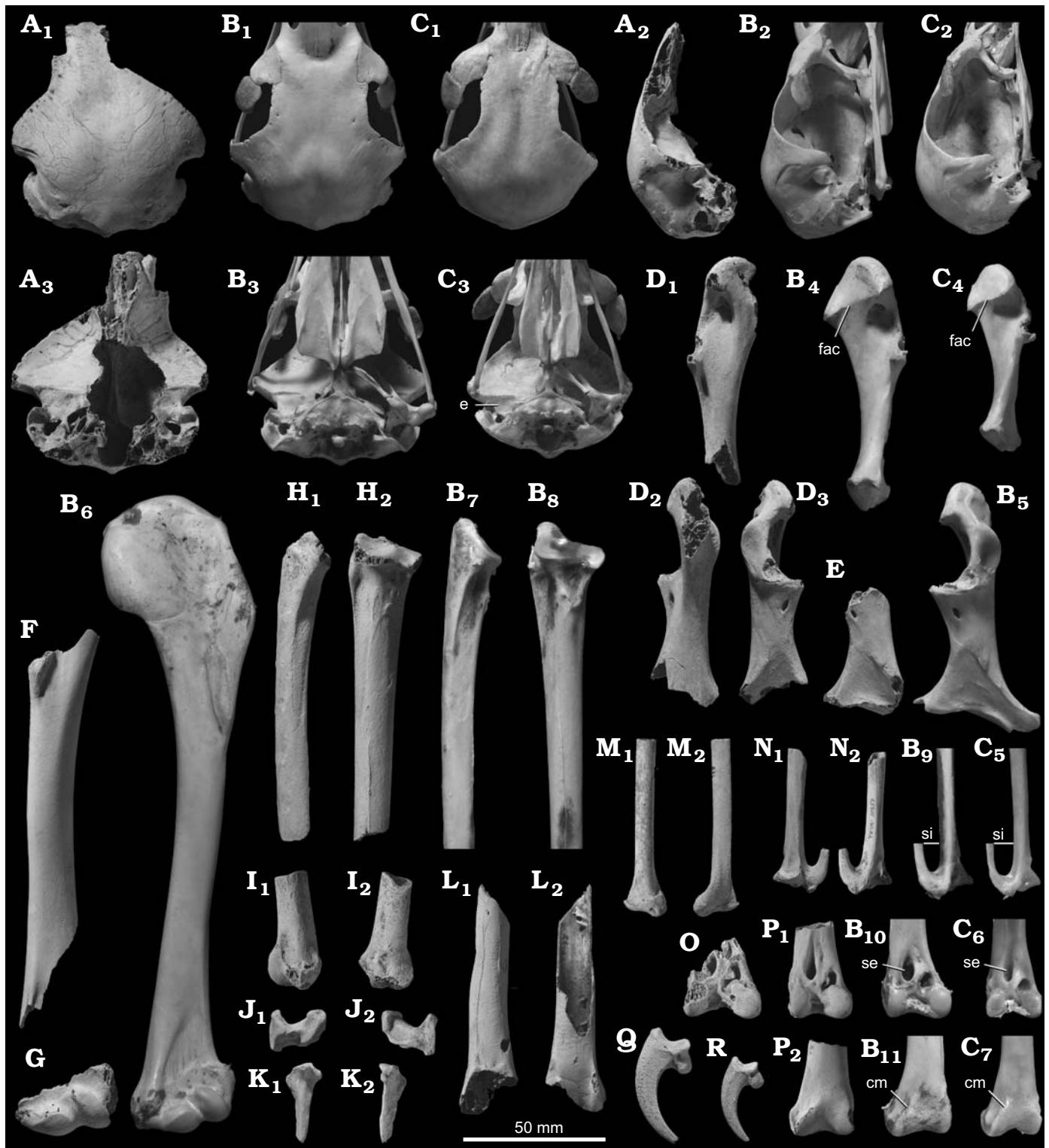
leucocephalus, and *H. pelagicus*. Other qualitative features, including a strong constriction of the cotyla dorsalis in its ventral part (less apparent in, e.g., *Harpia*, *Stephanoaetus*, and *Aquila*) and the lack of pneumatic foramina in the proximal end (foramina pneumatica are present caudal to the proximal articular surfaces and/or around the impressio m. brachialis in Gypini), are consistent with the assignment to *Haliaeetus*.

Two distal ends of carpometacarpi, one of which preserves the distal part of the os metacarpi minor near the distal symphysis, are referred to this species (Fig. 8N). So far as observed in the better preserved specimen, the spatium intermetacarpale is craniocaudally narrow, as characteristically observed in *Elanus*, *Kaupifalco*, *Butastur*, and *Haliaeetus* (Fig. 8B₉, C₅). The fossils further differ from

Gypini in the absence of foramina pneumatica at or around the distal symphysis.

Five distal ends of the tibiotarsus are referred to this species (Fig. 8O, P). In the fossils, the sulcus extensorius is lying near the lateral margin of the distal shaft, and almost restricted to the lateral half of the bone, agreeing with *Circus*, *Accipiter*, *Haliaeetus* (except *H. leucogaster*), *Icthyophaga*, and perhaps *Aquila* (the condition is less clear in the last genus; Fig. 8B₁₀, C₆). Among these genera, the fossils differ from *Circus*, *Accipiter*, and *Aquila* and agree with *Haliaeetus* and *Icthyophaga* in weak proximal extension of the medial margin of the condylus medialis on the caudal surface; in the former group, the margin clearly extends past the proximal margin of the condyle on the cranial side (Fig. 8C₇), whereas it fades more distally in the latter

Fig. 8. Accipitrid bird *Haliaeetus* sp. from the middle–upper Pleistocene of Shiriya, Japan (A, D–R), compared with Recent *Haliaeetus pelagicus* (Pallas, 1811) from Japan (B) and Recent *Aquila chrysaetos* (Linnaeus, 1758) from Japan (C). **A.** NSMT PV 24581, cranium in dorsal (A₁), right lateral (A₂), and ventral (A₃) views. **B.** NSMT AS 1344, cranium in dorsal (B₁), right lateral (B₂), and ventral (B₃) views; right coracoid in medial (B₄) and dorsal (B₅) views; left humerus in cranial view (B₆); left ulna in ventral (B₇) and cranial (B₈) views; left carpometacarpus in ventral view (B₉); left tibiotarsus in cranial (B₁₀) and caudal (B₁₁) views (reversed for comparison). **C.** NSMT AS 1299, cranium in dorsal (C₁), right lateral (C₂), and ventral (C₃) views; right coracoid in medial view (C₄); left carpometacarpus in ventral view (C₅); left tibiotarsus in cranial (C₆) and caudal (C₇) views (reversed for comparison). →



D. NSMT PV 24556, left coracoid in medial (D_1), ventral (D_2), and dorsal (D_3) views. **E.** NSMT PV 24557, right coracoid in dorsal view. **F, G.** NSMT PV 24582 and NSMT PV 24558, respectively, right and left humeri in cranial view. **H, I.** NSMT PV 24584 and NSMT PV 24562, respectively, left ulnae in ventral (H_1 , I_1), cranial (H_2), and dorsal (I_2) views. **J.** NSMT PV 24586, left ulnare in proximal (J_1) and distal (J_2) views. **K.** NSMT PV 24565, left alular phalanx in dorsal (K_1) and ventral (K_2) views. **L.** NSMT PV 24587, left femur in caudal (L_1) and cranial (L_2) views. **M.** NSMT PV 24585, left radius in caudal (M_1) and cranial (M_2) views. **N.** NSMT PV 24564, left carpalometacarpus in dorsal (N_1) and ventral (N_2) views. **O.** NSMT PV 24591, right tibiotarsus in cranial view. **P.** NSMT PV 19010, left tibiotarsus in cranial (P_1) and caudal (P_2) views. **Q, R.** NSMT PV 24570 and NSMT PV 24571, respectively, terminal phalanges of right second and third pedal digits in medial view. Fossils coated with ammonium chloride. Abbreviations: cm, (proximal extent of the caudal margin of) condylus medialis; e, excavation rostral to the tympanic cavity (see text); fac, (sternal margin of) facies articularis clavicularis; se, sulcus extensorius; si, spatium intermetacarpale.

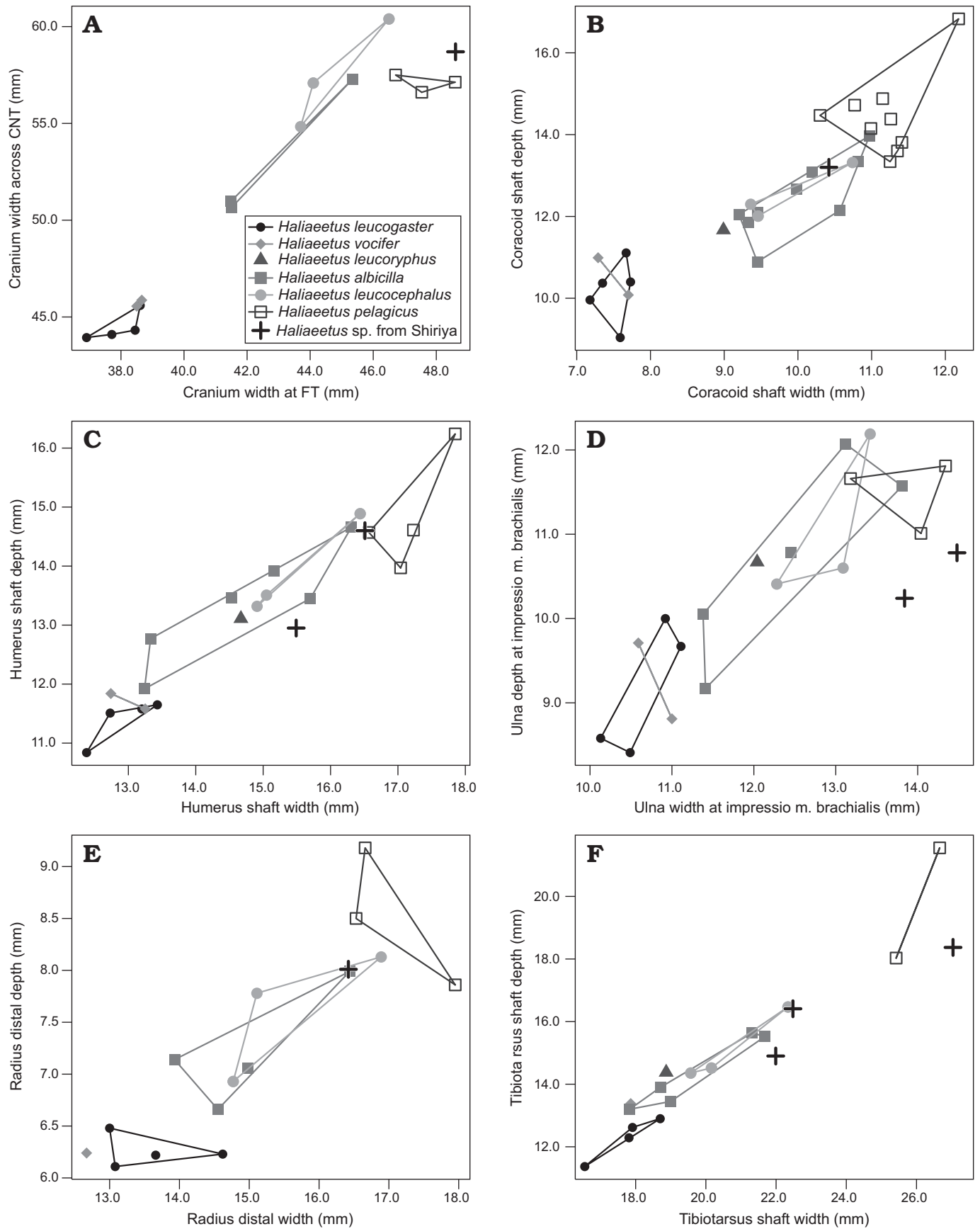


Fig. 9. Bivariate scatter plots of Recent and fossil species of *Haliaeetus*: cranial (A), coracoidal (B), humeral (C), ulnar (D), radial (E), and tibiotarsal (F) measurements. Abbreviations: CNT, crista nuchalis transversa; FT, fossa temporalis.

group (Fig. 8B₁₁). The tibiotarsus of *Aquila* further differs in a much deeper incisura intercondylaris (Fig. 8C₆, C₇). The tibiotarsus of *Ichthyophaga* differs in a distinctly deeper, wider sulcus extensorius.

Two shafts and two distal fragments of the humerus (Fig. 8F, G), one distal end of the ulna (Fig. 8I), three ulnar shafts, one distal end of the radius (Fig. 8J), one complete ulnare (Fig. 8J), one alular phalanx lacking the distal tip (Fig. 8K), one distal shaft of the femur (Fig. 8L), one basal phalanx of the third toe, and 19 terminal phalanges of various toes (Fig. 8Q, R) are tentatively referred to this species based on their large size. Although the preserved parts carry little taxonomic information, some of these elements can be differentiated at least from other large accipitrids. In the fossil humerus, the proximal part of the condylus dorsalis does not possess a sharp, straight ventral margin (which is observed in *Aegypius*). The fossil distal ulna, radius, ulnare, and alar phalanx differ from the corresponding elements of Gypini in the absence of extensive pneumatization. From *Aquila*, the radius differs in a ventrally positioned caudal knob of the distal articular surface, the ulnare does in strongly convex distal margin of the facies articularis ulnaris, the alular phalanx in a relatively proximal position of the tubercle on the ventrocaudal margin near the proximal end (in *Aquila*, the tubercle is elongated distally), and the femur in a more strongly developed impressio anae m. iliofibularis near the proximal extent of the condylus lateralis.

Remarks.—The material examined here includes the specimen figured as *H. cf. pelagicus* (NSMT PV 19010) by Hasegawa et al. (1988). The size variation within the material seems to be consistent with the presence of only one species, although the possibility that more species are represented cannot be ruled out. With 35 identifiable specimens, the species is the most common landbird species represented in the Shiriya material (minimum number of individuals being three for Loc. 2 and one for each of Locs. 1 and 3). As far as concerning the elements preserved, it was difficult to find unambiguous osteological features that allow assignment to certain clades within the family. Nevertheless, most elements of the Shiriya material could be differentiated from those of other large eagles, *Aquila* and Gypini, thus they most likely represent a sea eagle of the genus *Haliaeetus*. Three modern species of *Haliaeetus* occur on the central Japanese islands today (The Ornithological Society of Japan 2012): *H. albicilla*, *H. pelagicus*, and *H. leucocephalus* (although the last species has only been recorded as an accidental visitor). Partly due to the small size of the comparative material, it is at best difficult to assign the material to any of these three species (see Fig. 9). Hence, it seems justified to leave the specific identification open rather than designating a particular species as was done by Hasegawa et al. (1988), pending further study.

The oldest putative records of the genus include a large accipitrid from the lower Oligocene of Egypt (Accipitridae genus and species indeterminate, aff. *Haliaeetus* in Rasmussen et al. 1987) and *Haliaeetus* (?) sp. from the middle Miocene

of Florida (Becker 1987a, b), whose true affinities are difficult to evaluate from the evidences provided. Neogene records include *H. piscator* Milne-Edwards, 1871, from the upper Miocene of France (Milne-Edwards 1867–1871), and *H. fortis* Kurochkin, 1985, from the upper Miocene–lower Pliocene of Mongolia (Kurochkin 1985; Zelenkov 2013). It should be noted that the placement of the former species within *Haliaeetus* has been doubted by Mlíkovský (2002). According to published dimensions and illustrations, both *H. piscator* and *H. fortis* seem to have been smaller than the species represented by the Shiriya material.

A putative Early Pleistocene species from Czech Republic, *H. angustipes* Jánossy, 1983, has been shown to be inseparable from modern *H. albicilla* by Mlíkovský (1997). An extinct species *H. australis* (Harrison and Walker, 1973) is known from the Holocene of the Chatham Islands (Dawson 1961; Harrison and Walker 1973; Olson 1984; Millener 1999). Published dimensions of that species (Harrison and Walker 1973) suggest that it might be comparable in size with the Shiriya material, but it is not feasible to make a comparison because the latter lacks the tarsometatarsus, the most intensively described element of *H. australis* (Harrison and Walker 1973; Olson 1984). A genetically distinct lineage which is most closely related to *H. albicilla* is known from Holocene deposits of Hawaiian Islands (Olson and James 1991; Fleischer et al. 2000; Hailer et al. 2015). Published dimensions of the Hawaiian material (Olson and James 1991) indicate that it is smaller than the Shiriya material.

Occurrence of modern species of the genus has been recorded from various Pleistocene localities. *Haliaeetus albicilla* and *H. leucogaster* are known from numerous localities in the Old World (e.g., Hou 1993; Tyrberg 1998, 2008a; Guerra et al. 2013; Huguet et al. 2017) and North America (e.g., Brodkorb 1964; Guthrie 1992; Emslie 1998), respectively. *Haliaeetus vocifer* has been recorded from a few localities in Africa, whereas *H. vociferoides* has been recorded from Madagascar (Lambrecht 1933; Phillips 1988). Baird (1991) mentioned the occurrence of cf. *H. leucogaster* from Quaternary cave deposits in Australia. Apparently, *H. pelagicus* does not have a definitive fossil record, apart from Holocene archaeological occurrences (e.g., Friedman 1935). Although Rich et al. (1986) cited the occurrence of *H. cf. pelagicus* from the Pleistocene of Yage, central Honshu Island, the original report of the site (Tomida 1978) designated the relevant species as *Haliaeetus* sp. indet. Further work with larger comparative material would be required to verify the identifications of the putative records of the last species, whose breeding range is largely restricted around the Sea of Okhotsk today.

Accipitridae gen. et sp. indet.

Fig. 10.

1988 *Buteo buteo* (Linnaeus, 1758); Hasegawa et al. 1988: pl. 7: 6.

Material.—Loc. 3, Shiriya, Aomori Prefecture, Japan; Late Pleistocene (~MIS 5e): NSMT PV 19003, right femoral shaft;

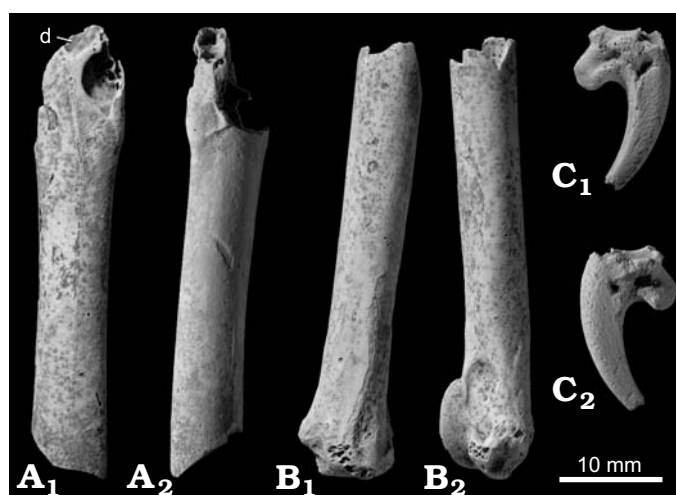


Fig. 10. Accipitridae gen. et sp. indet. from the upper Pleistocene of Shiriya, Japan. **A.** NSMT PV 19003, left femur in cranial (A₁) and lateral (A₂) views. **B.** NSMT PV 24599, left ulna in craniodorsal (B₁) and ventral (B₂) views. **C.** NSMT PV 24598, terminal phalanx of (right second?) pedal digit in lateral (C₁) and medial (C₂) views. Fossils coated with ammonium chloride. Scale bar 10 mm. Abbreviation: d, depression proximal to foramen pneumaticum (see text).

NSMT PV 24598, terminal phalanx of pedal digit (right second?). Locality unrecorded, Shiriya, Aomori Prefecture, Japan; Middle–Late Pleistocene (~MIS 9/5e): NSMT PV 24599, left distal ulna.

Measurements.—See Table 5; no formal measurement was possible for the pedal phalanx.

Description.—One moderately worn distal ulna was recovered (Fig. 10B). In the fossil, the proximal margin of the trochlea carpalis is strongly elevated from the shaft, agreeing with *Nisaetus*, *Kaupifalco*, *Melierax*, *Circus*, *Accipiter*, and *Buteo* (and perhaps with *Butastur*, to a lesser extent). Concerning these genera, the fossil differs from *Melierax* in a proximally elongated trochlea carpalis, from *Kaupifalco* and *Accipiter* in the absence of a deep fossa ventral to the trochlea carpalis. In addition, the ulna of *Accipiter* differs in a long, sharp, and longitudinally oriented tip of the tuberculum carpalis. Therefore, the fossil probably represents a species of *Nisaetus*, *Circus*, or *Buteo*, but further identification does not seem feasible.

One fragmentary shaft of the femur preserving a foramen pneumaticum (Fig. 10A) and one terminal pedal phalanx,

Table 5. Measurements (in mm) of Accipitridae gen. et sp. indet. from the upper Pleistocene of Shiriya. Abbreviations: D, craniocaudal (for ulna) or craniocaudal (for femur) depth; W, dorsoventral (for ulna) or mediolateral (for femur) width.

Elements	Measurements
Ulna	
distal W	8.6
distal D	9.1
Femur	
W midshaft	6.8
D midshaft	6.6

probably of the right second toe (Fig. 10C), were recovered. The only notable feature of these fossils is the presence of a depression just proximal to the foramen pneumaticum medial to the crista trochanteris of the femur (Fig. 10A). This feature is observed in *Macheiramphus*, *Kaupifalco*, *Melierax*, *Circus*, and *Buteo*.

Remarks.—It is obvious that the three specimens represent one or more species much smaller than *Haliaeetus* sp. described above. Although the femur, NSMT PV 19003, was figured as *Buteo buteo* by Hasegawa et al. (1988), it is too fragmentary and not diagnostic enough to allow identification to the generic level. Even assuming that the ulna and femur represent the same species, they may possibly represent either *Circus* or *Buteo*, each of which includes several modern species distributed on the central Japanese islands today. Therefore, it seems reasonable to retract the record of *B. buteo* from the Shiriya local fauna.

Concluding remarks

The present analysis of the avian remains from the Shiriya local fauna, northeastern Honshu Island, Japan, indicated the presence of six species of non-passeriform landbirds: *Syrnaticus* sp., Coturnicini gen. et sp. indet., Columbidae gen. et sp. indet., *Apus* sp., *Haliaeetus* sp., Accipitridae gen. et sp. indet. Species-level identification for the landbird remains was not feasible with the comparative materials examined in this study, unless it is assumed that only species occurring in this area today are represented. Such an assumption may potentially lead to circular reasoning in biogeographic and/or paleoclimate analyses, thus was not attempted here (see above). Indeed, when seabirds are taken into account, the Shiriya paleoavifauna includes an extralimital cormorant species (Watanabe et al. 2018) and at least three other extinct species (Hasegawa et al. 1988; Watanabe and Matsuoka 2015; Watanabe et al. 2016; JW, HM, and YH unpublished material). Nevertheless, the occurrences of the six landbird taxa are not unexpected, given that their relatives are members of the modern avifauna in the area. This is in contrast to the land mammal fauna recovered from the Shiriya localities (and Late Pleistocene localities on Honshu Island in general), which includes several extinct members of taxa that are not seen in the area today, including an elephant *Palaeoloxodon naumanni*, large deer *Sinomegaceros yabei*, and tiger *Panthera tigris* (e.g., Hasegawa 1972; Hasegawa et al. 1988; Iwase et al. 2012).

Although little is known about the Pleistocene terrestrial paleoclimate in northern Honshu Island, especially concerning the age of the Shiriya localities (MIS 9/5e), some information is available for central Honshu Island, where continuous records of lacustrine sediments exist (e.g., Tarasov et al. 2011; Kigoshi et al. 2017). Palynological analyses of such sediments have reconstructed that the climate in the last few interglacial periods, including MISs 9 and

5e, is slightly to considerably cooler (by up to ~4°C) than, and characterized by a comparable amount of precipitation to, the present (Tarasov et al. 2011; Kigoshi et al. 2017). If such conditions were also prevalent in northern Honshu Island, the Shiriya landbird fauna likely resided in such an environment. One remarkable element is *Syrmaticus*, whose modern species are generally associated with mountainous forests (Johnsgard 1999). The presence of *Syrmaticus* sp. in Shiriya may imply the presence of such a habitat in northern Honshu Island in the last interglacial period (MIS 5e) as is seen today. In addition, the presence of *Syrmaticus* may have some biogeographic implications. Modern *S. soemmerringii*, the only species of the genus occurring on the Japanese islands today, does not occur north to the Tsugaru Strait (i.e., on Hokkaido Island), the fact which was originally used to substantiate the biogeographic delineation now known as Blakiston's line (Blakiston and Pryer 1880; Blakiston 1883). If *Syrmaticus* sp. from the Shiriya local fauna had similar climatic requirements to those of the modern species, it may follow that the northern distribution limit of the modern species is at least partly influenced by factors other than climatic ones (temperature), as *Syrmaticus* sp. from Shiriya could inhabit the northern end of Honshu Island in a colder climate condition than in the present. That is, the Tsugaru Strait may have acted as a biogeographic barrier that prevented northward dispersals to Hokkaido Island by *Syrmaticus*. If they could cross the strait to colonize Hokkaido Island in the last glacial period, as was apparently done by some large land mammals in the opposite direction (Kawamura 2007), they would have been able to persist there. Nevertheless, the possibility remains that they retreated southward in glacial periods. A more substantiated discussion may be possible after species-level identification could be made with a larger comparative material, and evidences from other fossil localities were accumulated.

Apart from species-level identifications, the landbirds identified from the Shiriya local fauna in this study add new pieces to the Pleistocene vertebrate community in northern Honshu Island. *Syrmaticus* sp., Coturnicini gen. et sp. indet., and Columbidae gen. et sp. indet. are likely to have been primarily granivorous or frugivorous birds as in the modern representatives of the taxa, and might have interacted with the diverse assemblage of rodents and shrews known from the same local fauna (Hasegawa et al. 1988). Accipitridae gen. et sp. was probably an aerial predator that preyed on such small vertebrates (possibly along with invertebrates). *Haliaeetus* sp. might have relied more on marine preys, such as a salmonid fish *Oncorhynchus* sp. which was identified from Loc. 3 (Hasegawa et al. 1988). *Apus* sp. would have been an aerial insectivore, and in this respect an indirect interaction with insectivorous bats in the local fauna (Hasegawa et al. 1988) could be presumed, although direct competition would have been mitigated by the difference in diel activity patterns (diurnal swift versus nocturnal bats).

By describing six species of landbirds from the Pleistocene of Shiriya, this study formed a basis for comparison in

future studies of the Pleistocene fossil birds in the Japanese Archipelago. Revision of avian materials from other Pleistocene localities in the region (Takai 1962; Hasegawa 1964; Tomida 1978; Nokariya and Ono 1980; Ono 1980; Rich et al. 1986) may shed more light on the biogeographic history of the landbird fauna. One pertinent problem is, however, the scarcity of avian skeletons from the eastern Eurasia and Japanese islands in the museum collections, which was partly responsible for the inconclusive identifications in this study. It is urgent to build larger skeletal collections of birds from the eastern Eurasia, in order to fully appreciate contemporary variation within and among modern forms, and to decipher history of the unique avifauna in the region.

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Appendix 1

List of comparative materials examined; specimens are listed by species/subspecies and then geographic regions. Sex composition and number of partial skeletons are given in parentheses (m, male; f, female, u, unsexed; p, partial skeleton).

Phasianidae.—*Rollulus rouloul*: aviary, MVZ 59088 (m). *Arborophila brunneopectus*: Thailand, USNM 343998 (f). *Afropavo congensis*: aviary, USNM 430171 (m). *Pavo cristatus*: aviary, MVZ 179393, USNM 289970, 321837, UWB 116856 (3 m, 1 f). *Argusianus argus*: Thailand, USNM 19471 (u); aviary, UWB 85092 (f). *Polyplectron napoleonis*: aviary, USNM 621671, 621673, UWB 82965 (2 m, 1 f). *Coturnix coturnix*: aviary, MVZ 136488 (m). *Coturnix japonica*: Mongolia, UWB 59843 (m); Korea, USNM 633328 (f); aviary, USNM 343450, 344514 (1 m, 1 f). *Coturnix coromandelica*: aviary, MVZ 134780 (m). *Synoicus ypsilophorus*: New Guinea, USNM 53359 (m). *Synoicus chinensis*: New Guinea, MVZ 149273 (m); Philippines, USNM 562143, 562145 (2 m). *Tetraogallus himalayensis*: aviary, USNM 430182, UWB 65198 (1 m, 1 f). *Alectoris chukar*: Israel, USNM 605025, 605030 (2 f); aviary, MVZ 31125 (m). *Ammoperdix heyi*: Israel, USNM 605023 (f). *Perdica asiatica*: aviary, USNM 491899 (u). *Pternistis capensis*: South Africa, USNM 558454, 558460 (1 m, 1 f). *Pternistis afer*: Zimbabwe, USNM 488838, 489335 (1 m, 1 f). *Francolinus pintadeanus*: Thailand, USNM 343198, 343199 (2 m). *Dendroperdix sephaena*: Tanzania, USNM 634713, 634721 (1 m, 1 f). *Peliperdix lathamii*: Cameroon, USNM 291780 (m). *Scleroptila lewaillantii*: South Africa, USNM 489466 (m). *Scleroptila afra*: South Africa, UWB 53131 (m). *Bambusicola thoracicus*: China, USNM 318518, 318741 (1 m, 1 f); Japan (introduced), MVZ 128713 (m). *Bambusicola sonorivox*: Taiwan, USNM 611819 (f). *Gallus gallus*: Indonesia, USNM 560790 (f); aviary, MVZ 12495, 45503 (2 u). *Lophophorus impejanus*: aviary, MVZ 137892, USNM 631757, 638632, UWB 84421 (2 m, 2 f). *Tragopan temminckii*: aviary, USNM 491867, 621027 (1 m, 1 f). *Tragopan caboti*: aviary, MVZ 45525, 53922 (2 f). *Ithaginis cruentus*: China, USNM 319182 (m); Tibet, USNM 319189 (f). *Pucrasia macrolopha*: aviary, UWB 57088 (m). *Syrnaticus ellioti*: aviary, UWB 33449, 82958 (2 m). *Syrnaticus humiae*: aviary, USNM 615083, UWB 82957 (2 m). *Syrnaticus mikado*: aviary, USNM 346556, UWB 58985 (1 m, 1 f). *Syrnaticus soemmerringii*: aviary, MVZ 46111, 49764, USNM 292907, 292968, 344667 (3 m, 1 f, 1 u). *Syrnaticus reevesii*: aviary, USNM 289572, 290302, 290303, 320867, 322767, 344402, 346350, 428249, 500369, 500710 (8 m, 3 f). *Chrysolophus pictus*: aviary, MVZ 138007, 136614, UWB 119203 (3 m). *Chrysolophus amherstiae*: aviary, UWB 73867 (f). *Phasianus colchicus*: Korea, USNM 633483, 633485 (1 m, 1 f); California (introduced), MVZ 51673, 51673A, 68327, 84651, 133528, 135071, 156120, 176024 (4 m, 3 f). *Crossoptilon crossoptilon*: China, USNM 319197, 319200 (1 m, 1 u); aviary, USNM 554966 (f). *Crossoptilon mantchuricum*: aviary, MVZ 53980, USNM 320973 (1 m, 1 f). *Crossoptilon auritum*: aviary, MVZ 137900 (m). *Catreus wallichii*: aviary, USNM 346852, 347598 (2 f). *Lophura swinhoii*: aviary, USNM 320294, 343428 (1 m, 1 f). *Lophura erythrophthalma*: aviary, MVZ 56240 (m). *Perdix perdix*: Canada, MVZ 140248, USNM 641454, 641462 (1 m, 2 f). *Meleagris gallopavo*: California, MVZ 183406, 183408, 183409 (2 m, 1 f); New York, USNM 556325 (f). *Bonasa umbellus*: Canada, MVZ 15546, 68068 (1 m, 1 f). *Bonasa bonasia*: Siberia, USNM 557496, 557499 (1 m, 1 f). *Lagopus muta*: Sweden, USNM 620108 (m); Alaska, MVZ 137293 (f). *Dendragapus obscurus*: Nevada, MVZ 151729, 151733 (2 f);

California, USNM 630803 (f). *Falcipennis falcipennis*: Primorye, USNM 622432 (f). *Falcipennis canadensis*: Canada, MVZ 63067 (f); Idaho, MVZ 61793 (m). *Lyrurus tetrix*: Kalininskaya, USNM 500266 (m). *Centrocercus urophasianus*: Montana, USNM 17707 (f); Nevada, MVZ 151737, 151739 (1 m, 1 f). *Tympanuchus phasianellus*: South Dakota, USNM 559925 (m). *Tympanuchus pallidicinctus*: Kansas, MVZ 98474, 13175 (1 m, 1 f).

Columbidae.—*Columba livia*: California (introduced), MVZ 129295, 129298 (1 m, 1 f). *Columba rupestris*: Korea, MVZ 135053 (m). *Columba leuconota*: aviary, MVZ 30684 (f). *Columba guinea*: aviary, MVZ 29113 (m). *Columba palumbus*: France, MVZ 141896 (m). *Columba arquatrix*: South Africa, MVZ 158703 (m). *Streptopelia orientalis*: Japan, MVZ 123361, 128741 (1 m, 1 f). *Streptopelia decaocto*: Korea, MVZ 142609, 142610 (1 m, 1 u). *Streptopelia semitorquata*: South Africa, MVZ 158704 (m). *Streptopelia capicola*: South Africa, MVZ 158705 (f). *Spilopelia chinensis*: Australia, MVZ 143413 (m); aviary, MVZ 41184. *Spilopelia senegalensis*: Botswana, MVZ 158706 (f); South Africa, MVZ 158707 (m). *Macropygia unchall*: locality unknown, MVZ 43622, 46152 (2 f). *Macropygia phasianella*: Australia, MVZ 142187 (m); aviary, 54636 (m). *Ectopistes migratorius*: locality unknown, MVZ 84315 (u). *Patagioenas leucocephala*: aviary, MVZ 138015 (f). *Patagioenas plumbea*: Peru, MVZ 165113 (u). *Patagioenas fasciata*: California, MVZ 54522, 65175 (1 m, 1 f). *Patagioenas cayennensis*: Panama, MVZ 154938 (f). *Patagioenas flavirostris*: Mexico, MVZ 74760, 78703 (1 m, 1 f). *Starnoenas cyanocephala*: aviary, MVZ 41332 (f). *Geotrygon chrysia*: aviary, MVZ 45593 (f). *Leptotila verreauxi*: Mexico, MVZ 74761 (m); El Salvador, MVZ 85621 (f). *Zenaidura macroura*: Colombia, MVZ 141733 (m). *Zenaidura asiatica*: Arizona, MVZ 68837 (f); Mexico, MVZ 51073 (m). *Zenaidura galapagoensis*: Galapagos, MVZ 140769, 140958 (1 m, 1 f). *Zenaidura auriculata*: Colombia, MVZ 94080, 94081 (2 m). *Zenaidura macroura*: Arizona, MVZ 151848 (f); Kansas, MVZ 65118 (m). *Zenaidura graysoni*: aviary, MVZ 46606 (f). *Columbina inca*: Mexico, MVZ 74762, 153894 (1 m, 1 f). *Columbina picui*: Paraguay, MVZ 168806 (f); Bolivia, MVZ 141731 (f). *Columbina cruziana*: aviary, MVZ 74908 (f). *Claravis pretiosa*: El Salvador, MVZ 85615, 85616 (1 m, 1 f). *Henicophaps albifrons*: aviary, MVZ 44278, 46012 (1 f, 1 u). *Gallinula lucionica*: aviary, MVZ 47109, 53804 (1 m, 1 f). *Gallinula rufifrons*: aviary, MVZ 49759 (m). *Alopecoenas jobiensis*: aviary, MVZ 47105, 51344 (1 m, 1 u). *Alopecoenas xanthonurus*: Mariana Islands, MVZ 115697 (m). *Alopecoenas rubescens*: aviary, MVZ 44500, 46017 (2 f). *Alopecoenas canifrons*: Palau Islands, MVZ 95122 (m). *Alopecoenas starii*: aviary, MVZ 51708 (m). *Leucosarcia melanoleuca*: Australia, UWB 62821, 62938 (2 f). *Geophaps plumifera*: aviary, MVZ 136616, 136617 (1 m, 1 f). *Phaps chalcoptera*: Australia, MVZ 154306 (m); aviary, MVZ 53809 (f). *Phaps elegans*: aviary, MVZ 30693, 133589 (1 f, u). *Phaps histrionica*: Australia, MVZ 141935 (m). *Ocyphaps lophotes*: Australia, MVZ 143420 (m); California, MVZ 88909 (f). *Geopelia striata*: Australia, MVZ 142189, 143414 (1 m, 1 f). *Otidiphaps nobilis*: aviary, MVZ 46124 (u). *Goura cristata*: aviary, MVZ 42673, 133590 (1 m, 1 f). *Didunculus strigirostris*: aviary, MVZ 27595 (f). *Turtur afer*: aviary, MVZ 40448 (f). *Turtur brehmeri*: Ghana, MVZ 164175 (f). *Oena capensis*: South Africa, MVZ 158709 (m). *Treron axillaris*: aviary, MVZ 27141 (m). *Duc-*

ula aenea: aviary, MVZ 51705 (u). *Ducula pacifica*: Samoa, MVZ 65412, 65409 (u). *Ducula latrans*: Fiji, MVZ 51372, 51373 (1 m, 1 f). *Ducula bicolor*: aviary, MVZ 50566, 50570 (1 m, 1 f). *Megaloprepia magnifica*: New Guinea, MVZ 149287, 149288 (1 m, 1 f). *Chrysoena viridis*: Solomon Islands, MVZ 93619 (m). *Ptilinopus solomonensis*: Bismark Archipelago, MVZ 93389 (m). *Ptilinopus ornatus*: New Guinea, MVZ 149284 (m). *Ptilinopus perlatus*: New Guinea, MVZ 149285, 149286 (2 m). *Ptilinopus insolitus*: Bismark Archipelago, MVZ 93390 (f). *Ptilinopus roseicapilla*: Marianas Islands, MVZ 115695 (f). *Ptilinopus porphyraceus*: Samoa, MVZ 65418 (m). *Hemiphaga novaeseelandiae*: New Zealand, MVZ 80402 (f). *Lopholaimus antarcticus*: Australia, MVZ 154297 (f).

Apodidae.—*Cypseloides niger*: Alaska, MVZ 39795 (m); Washington, UWB 19444, 21286, 33110, 91683 (3 m); Oregon, UWB 59363 (f); Dominican Republic, USNM 290999 (m); locality unknown, UWB 19444 (u). *Streptoprocne rutila*: Venezuela, USNM 614122 (m). *Streptoprocne phelpsi*: Guyana, USNM 622775 (m). *Streptoprocne zonaris*: El Salvador, MVZ 85724 (m); Colombia, MVZ 120732 (f). *Streptoprocne semicollaris*: Mexico, MVZ 152986, USNM 489351 (1 m, 1 f). *Chaetura spinicaudus*: Guyana, USNM 637197 (f). *Chaetura cinereiventris*: Costa Rica, MVZ 155742, 155743 (2 f). *Chaetura vauxi*: Washington, UWB 48231, 48232, 48237 (1 m, 2 f); Oregon, UWB 42223 (m); California, MVZ 41027 (f); El Salvador, MVZ 85721 (m). *Chaetura pelagica*: Florida, MVZ 53252–53256, 66685 (1 m, 5 f); Honduras, UWB 32456 (u). *Hirundapus caudacutus*: Russia, UWB 46916, 47128, 47230, 47231, 47345, 57445 (3 m, 3 f); Japan, USNM 500799, YIO 65584, 65584 (2 m, 1 f). *Hirundapus cochinchinensis*: Thailand, MVZ 156689 (u). *Hirundapus giganteus*: Thailand, MVZ 156688 (u). *Collocalia troglodytes*, Philippines, USNM 430517 (f). *Collocalia esculenta*, Philippines, USNM 635376 (f); Solomon Islands, UWB 63237, 63239 (2 f). *Aerodramus hirundinaceus*: Papua New Guinea, MVZ 149295 (f). *Aerodramus sawtelli*: Cook Islands, UWB 42487, 42488, 42541–42543, 42565–42567 (2 m, 5 f, 1 u). *Aerodramus inquietus*: Pohnpei Island (Caroline Islands), USNM 431409 (m). *Aerodramus bartschi*: Mariana Islands, MVZ 95143 (f); Guam, MVZ 115703, 115704, 115713–115717 (5 m, 2 f). *Aerodramus spodiopygius*: Fiji, MVZ 51721–51723 (1 m, 1 f, 1 u); New Caledonia, USNM 561598 (m). *Aeronautes saxatalis saxatalis*: Washington, UWB 40650, 42303, 54112, 54113, 55981, 55982 (4 m, 2 f); California, MVZ 41907, 77721–77723 (3 m, 1 f); Montana, MVZ 28986 (m); Arizona, UWB 33227, 34155, 34156 (1 m, 1 f, 1 u). *Tachornis phoenicobia*: Dominican Republic, USNM 555775 (m). *Tachornis squamata*: Guyana, USNM 621960 (m). *Panyptila cayennensis*: Panama, USNM 431346 (u); Brazil, USNM 321670 (u). *Cypsiurus parvus*: Alaska, MVZ 67569 (f); Gabon, USNM 64851 (f). *Tachymarpis melba*: Crete, USNM 559068 (u). *Apus pacificus*: Russia (ssp. *pacificus*), USNM 500258, UWB 43827–43830, 44398, 44399, 46954–46956, 46958, 46959 (6 m, 6 f); Korea (ssp. *pacificus*), MVZ 148837 (m); Japan (ssp. *pacificus*?), YIO 63553, 63946 (1 m, 1 f); Taiwan (ssp. *kanoi* or *kurodae*?), YIO 48 (f). *Apus caffer*: South Africa, UWB 53219 (m). *Apus nipalensis*: Japan, YIO 63093 (u); Taiwan, USNM 611837 (m); Vietnam, USNM 431471, 431472 (2 m). *Apus affinis*: Cameroon, USNM 292415, 292416 (1 m, 1 f); São Tomé, USNM 614156, 614157 (2 u); Gabon, USNM 642847, 642848 (2 m). *Apus barbatus*: South Africa, UWB 52770 (m). *Apus apus*, Spain, UWB 1962 (u); France, UWB 32988 (u); Russia, UWB 56587, 56589 (1 m, 1 f); China, NSMT AS Morioka Collection unnumbered (u).

Accipitridae.—*Pandion haliaetus* (Pandionidae): Indonesia, USNM 560783 (f). *Elanus caeruleus*: South Africa, USNM 558445, 558447 (2 f). *Elanus leucurus*: California, USNM 19603 (u). *Gampsonyx swainsonii*: Guyana, USNM 623084, 623110 (1 m, 1 f). *Leptodon cayanensis*: Panama, USNM 613953 (m). *Pernis ptilorhynchus*: Nepal, USNM 620644 (u); Thailand, USNM 343983 (m). *Aviceda subcristata*: Indonesia, USNM 558306 (f); Australia, USNM 620187 (f). *Polyboroides typus*: Zimbabwe, USNM 430434, 430435 (1 m, 1 f). *Gypohierax angolensis*: Angola, USNM 18892 (u); French Congo, USNM 226143 (u). *Gypaetus barbatus*: Algeria, USNM 17834 (u); aviary, USNM 345684 (f). *Neophron percnopterus*: North Africa, USNM 17835 (u). *Spilornis cheela*: Thailand, USNM 19474, 343985 (1 m, 1 u). *Terathopius ecaudatus*: Tanzania, USNM 634509 (m). *Pitheophaga jefferyi*: Philippines, USNM 226900 (u, composite); aviary, USNM 499879 (m). *Circus cinereus*: Zimbabwe, USNM 430776 (m). *Trigonoceps occipitalis*: aviary, USNM 320859, 347358 (1 f, 1 u). *Necrosyrtes monachus*: Sudan, USNM 291440, 291443 (1 m, 1 f). *Gyps himalayensis*: Kashmir, USNM 19534 (m). *Gyps africanus*: Zimbabwe, USNM 431591 (f). *Aegyptius monachus*: Spain, USNM 614152 (u); China, USNM 289569 (u). *Macheiramphus alcinus*: Malaysia, USNM 559816 (u). *Harpia harpyja*: Aviary, USNM 429223, 429721 (2 f). *Stephanoetus coronatus*: aviary, USNM 345669, 346654 (1 m, 1 f). *Nisaetus cirrhatus*: aviary, USNM 344616 (m). *Aquila gurneyi*: Indonesia, USNM 554908 (u). *Aquila chrysaetos*: Tennessee, USNM 19394 (u). *Aquila audax*: Australia, USNM 620191, 620192 (1 m, 1 u). *Aquila verreauxii*: South Africa, USNM 612539 (u). *Aquila spilogaster*: Zimbabwe, USNM 430796, 490548 (1 m, 1 f). *Kaupifalco monogrammicus*: Liberia, USNM 347392, 347393 (1 m, 1 f). *Melierax metabates*: Zimbabwe, USNM 430326, 430381 (2 m). *Circus aeruginosus*: aviary, USNM 344419 (m). *Circus cyaneus*: California, USNM 610734 (f); Maryland, USNM 291684 (m). *Circus melanoleucos*: Russia, USNM 500257 (m). *Accipiter soloensis*: Indonesia, USNM 560782 (f). *Accipiter nisus*: Sweden, USNM 610363, 610366 (1 m, 1 f); China, USNM 290308 (f). *Accipiter gentilis*: Sweden, USNM 610353, 610358 (1 m, 1 f); Japan, USNM 499854 (u, p). *Haliaeetus leucogaster*: Indonesia, USNM 556992, 556993, 560784, 560785 (2 m, 2 f); aviary, YIO 60790 (m, p). *Haliaeetus vocifer*: Tanzania, USNM 488146 (m); Sudan, USNM 291449, 291450 (2 f). *Haliaeetus leucoryphus*: locality unknown, USNM 612540 (u). *Haliaeetus albicilla*: China, USNM 292774 (m); Korea, USNM 431363 (m); Japan, YIO 8974 (u, p); locality unknown, NSMT AS 578, 821, 874, 1197, NSMT PV 532, YIO 70778 (2 m, 3 u; 3 p). *Haliaeetus leucocephalus*: Alaska, USNM 489276, 615007, 615009 (2 m, 1 f). *Haliaeetus pelagicus*: Bering Island, USNM 17044 (u, p); Japan, YIO 8998, 8999 (1 m, 1 u; 2 p); aviary, YIO 9000, 15137 (1 m, 1 f; 2 p); locality unknown, NSMT AS 601, 620, 816, 1344, USNM 16959, YIO 70530 (6 u; 3 p). *Ichthyophaga ichthyaetus*: Sulawesi, USNM 224807 (m); aviary, USNM 468555 (u). *Haliastur sphenurus*: Australia USNM 610563 (m). *Haliastur indus*: Borneo, USNM 18759 (u); Indonesia, USNM 558303, 558304 (1 m, 1 f). *Milvus migrans*: Pakistan, USNM 557810 (f); Cameroon, USNM 291317 (m); China, USNM 292039, 319228, 319448 (1 m, 3 f). *Busarellus nigricollis*: Brazil, USNM 345772, 345773 (1 m, 1 f); aviary, USNM 431130 (f). *Geranospiza caerulescens*: Mexico, USNM 18450 (u); Brazil, USNM 345774 (m). *Butastur indicus*: Korea, USNM 18577 (u); Philippines, 611775 (f). *Ictinia plumbea*: Panama, USNM 613355, 613356 (2 m). *Buteo lagopus*: Sweden, USNM 610370 (f). *Buteo buteo*: China, USNM 292701, 318559–318561, 318739 (1 m, 2 f, 2 u).